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Smoking and health: time for a legal commitment

THE extent to which Mrs Thatcher's government is prepared to discourage smoking will become clear within the next few weeks. For by the end of March the UK government and the tobacco industry are due to have renewed their voluntary agreement on advertising. And on 26 March the tax on tobacco can be adjusted in the budget. It will be a great pity if either opportunity to discourage smoking is wasted.

Given that one in ten UK deaths can be directly attributed to smoking and that one smoker in four dies 10-15 years prematurely, there can be no question about whether smoking should be discouraged. The question is: how? There are three traditional answers. The first is to increase the price of tobacco, the second is to reduce advertising and the third is to educate the public on the dangers of smoking.

On the issue of price, the UK National Consumer Council has recently produced figures which show that, in real terms, the retail price of cigarettes in 1978 was only 76% of what it had been 10 years before. Given that price increases are commonly held to be the most effective and lasting way of reducing cigarette consumption, there is a very strong case at least for restoring the relative cost of smoking by increasing the tax on tobacco in the next budget.

The advertising of cigarettes is already limited by a voluntary agreement that was negotiated between government and industry in 1977. This stopped the advertising of cigarettes on television or during cinema performances to which the young were admitted. Other forms of advertising were not stopped but controls were placed on the image of smoking portrayed. It is difficult to prove that the level of advertising has any effect on the consumption of cigarettes rather than, as the industry argues, just on the choice of brands — but it seems prudent to assume it does. The immediate aim of the government should therefore be to limit advertising still further and ultimately to the point of sale. Furthermore, at the end of the year, the government should make the most of its opportunity to renegotiate the voluntary agreement on sponsorship of sport by the tobacco industry, a promotional exercise to the tune of an annual £10 million that has done much to associate smoking with health and youth in a way that advertising has not been allowed to do since 1977.

As for anti-smoking campaigns, on which the government spends something like one hundredth of the industry's budget for promotion, the cheapest and most direct way of publicising the hazards of smoking is on the cigarette packages themselves. There is much scope for expanding and varying the present trite warning that "cigarettes can seriously damage your health".

Any attempt to reduce the consumption of cigarettes,

however, needs to be complemented by efforts to reduce the risks to those who continue to smoke regularly. This currently includes 45% of male and 37% of female adults in the UK; the prevalence is falling but only markedly so in the higher socio-economic classes — for example among professional males the prevalence of smoking has fallen from 33% in 1972 to 25% now, whereas 60% of unskilled male manual workers still smoke compared with 64% in 1972.

One erstwhile promising approach to reducing the health hazards of smoking has clearly come to nothing. The idea was to replace some of the tobacco in cigarettes by a substitute that was, at best, harmless. A great deal of money was invested by the tobacco industry in the development of two tobacco substitutes. Early in 1977 the first report of the Independent Scientific Committee on Smoking and Health (the Hunter Committee) concluded that neither substitute was likely to be more harmful to health than tobacco alone and cigarettes containing them were launched in the UK later that year. But, as the recently published second report of the Hunter Committee says, sales of these cigarettes only briefly accounted for more than 2% of total sales.

Much greater success has met the introduction of low-tar brands of cigarettes and their acceptance by young smokers is probably the major cause of the declining trend in lung cancer deaths in UK males of less than 65 years of age. While welcoming the declining tar yields and recommending further substantial reductions, the second report of the Hunter Committee is less than forceful in its demands. It is left to the minority report of Dr J. D. Ball to point out that the average tar yield per cigarette sold in the UK has fallen very little since dropping 40% between 1965 and 1973. What is more disturbing is that the committee so strongly emphasises that reductions in tar yield will be limited by consumer acceptability of low-tar cigarettes. That appears to be a viewpoint that is more concerned with protecting the industry than it is with testing the limits of acceptability as a matter of urgency. Meanwhile the tobacco industry is apparently eager to spend £1 million on epidemiological studies of those who switch to low tar cigarettes rather than to admit that there is a case for reducing the tar levels now.

The attack on smoking can be pursued down a variety of paths, each one of which deserves to be explored vigorously. Voluntary agreements between government and industry are to be welcomed if they work — but there is considerable evidence that the tobacco industry has been less than scrupulous in honouring its commitments. That being so, the government should not be afraid to replace voluntary restrictions with legal ones if the tobacco industry is reluctant to agree to much stiffer controls on its distasteful business. □



United States

Environmentalists warn of continued threats to water supplies

DESPITE progress in reducing the more obvious sources of water pollution, US regulators are beginning to feel that problems in maintaining a clean and healthy water supply will play as controversial a role on the political agenda of the 1980s as the energy crises has done during the 1970s.

The latest warning of difficulties still to be faced comes from the Council on Environmental Quality, the watchdog committee established by President Nixon in 1970. In its latest annual report, published in Washington last week, the council says that the general standard of air quality has increased substantially over the past decade. In contrast progress in cleaning up water supplies has been far less impressive.

In particular, the council says that ground-water contamination from various activities, such as the use of pesticides in agriculture or the improper disposal of toxic wastes, is becoming a major problem for drinking-water supplies in parts of the country.

It draws attention to the impact of "acid rain" on wildlife and water quality; and looking ahead, picks out the problems of carcinogens in drinking water, supplies to "water-starved areas", and ageing distribution systems as three "basic and difficult problems" that the nation will have to face in the next few years.

Coming to grips with such problems may require new legislation and substantial resources: updating distribution systems, for example, could cost \$50 billion to \$100 billion nationwide to prevent large-scale disruption of supplies.

Yet left unsaid by the CEQ is that the Environmental Protection Agency is already struggling to carry out existing responsibilities which it has been given by Congress and in many cases the agency is meeting strong opposition from water utilities, who claim that new regulations to control toxic substances in water, for example, are over-restrictive and unnecessarily expensive.

Not that the picture is all gloom. The CEQ's report points out that there has been considerable success in controlling efficient emissions from factories and other identifiable industrial activities since the Clean Water Act was passed by Congress in 1973.

But statistics illustrate the severity of the problems that remain. Thus the report says that as many as two-thirds of the nation's lakes may have serious pollution problems and that an estimated 80% of the 37,700 lakes in urban areas in the US are

"significantly degraded".

This pollution is inevitably taking its toll of wild-life. In many lakes and rivers, toxic chemical contaminants such as PCBs have made fish inedible. Acid rain has made many lakes, particularly in the north-eastern United States, lethal to fish and other aquatic life and four million acres of commercial shell-fish waters have been closed.

The extent of the continuing pollution problem is also demonstrated by the fact that there has been "little or no overall change in the levels of five major water pollution indicators — fecal coliform bacteria, dissolved oxygen, total phosphorus content, total mercury, and total lead — over the four years 1975 to 1978, the CEQ reports.

Industry, in some ways a comparatively easy target for the EPA, has responded relatively well to control legislation. Although some industries, in particular the steel industry, have resisted stringent effluent restrictions, 90% of industrial discharges now meet "best practicable technology" standards laid down in 1977.

Municipalities responsible for water treatment have been more of a problem. Although federal funds have been made available for sewage treatment facilities since 1973, for example, many urban areas have been reluctant to take them up. Elsewhere construction projects have been plagued by cost-overruns and profiteering.

As a result, municipal sewage wastes are still "years away from being totally controlled" says the CEQ.

Furthermore both industry and water utilities are responding warily to what one EPA official refers to as the "second generation of water clean-up" shifting attention from more well-known and obvious pollutants to the long term effects

of relatively low levels of toxic substances.

The agency, for example, is already experiencing considerable difficulty in carrying out some of the requirements of the Safe Drinking Water Act of 1974, introduced after environmentalists found abnormally high cancer rates among residents of Louisiana who used water supplies from the Mississippi river.

Further difficulties are likely to face the EPA as it moves to implement industry-by-industry guidelines for the regulation of 129 top priority pollutants — mainly heavy metals and substances known or suspected to be carcinogenic — agreed after pressure from groups such as the Environmental Defense Fund to follow through on the agency's congressional mandate.

Then there is the growing problem of acid rain. This is caused when emission from automobiles or power-plants combines with water in the atmosphere.

Here the CEQ points out that in the eastern half of the US the acidity of rain-fall appears to have increased about 50-fold during the past 25 years. In addition to eliminating fish from lakes in the north-eastern US and Canada, acid rain, it says, "is also suspected of contributing to the leaching of toxic compounds into drinking water, especially surface water supplies".

All these problems are likely to mean increased responsibilities for the EPA. And the CEQ indicates that it is well aware of the difficulties faced, for example, in shifting the focus of control from point to "non-point" sources of pollution, such as run-off from construction sites, agricultural land or chemical dumps.

On top of all the other problems, the EPA is now faced with a bill introduced into the House of Representatives by Representative Phil Gramm of Texas, which would seriously limit its ability to enforce new quality controls: few believe the bill would pass solely on its technical merits but it could ride on the back of popular anti-regulatory sentiment and win a surprise victory.

David Dickson

Panel to assess formaldehyde health effects

THE US Consumer Product Safety Commission announced last week that it is to set up a panel to help assess the human implications of research findings that exposure to formaldehyde can cause cancer in laboratory rats. The panel will be established in conjunction with the National Toxicology Programme, and will be assembled from various federal health and safety agencies and scientific organisations.

Last October, scientists from the Chemical Industry Institute of Toxicology and the Formaldehyde Institute reported

that three laboratory rats of several hundred exposed to formaldehyde gas had developed prominent nasal cancers which were identified as squamous cell carcinoma.

Health scientists from CPSC and other regulatory agencies were told last month that such cancers were now evident in 37 of the rats in the study, which is three-quarters of the way through its two-year duration. In a random sample of rats selected for sacrifice and pathological examination after exposure at the dose level of 15 parts per million, 20% showed evidence of squamous cell carcinoma. □

Scientists protest at exclusion of Russians from conferences

US scientists reacted with anger and embarrassment last week to the decision by federal authorities to bar Soviet-bloc delegates from two scientific conferences, one on computer technology the other a joint conference on laser engineering and inertial confinement fusion.

The decision appeared to contradict earlier statements by the administration that, although cutting off high level exchanges with the USSR following the invasion of Afghanistan and the exile of Andrei Sakharov, it intended to maintain lower-level scientific links.

But administration officials point out that the decision to exclude Soviet participation was taken to restrict high technology exports.

Commerce and State Department officials, acting apparently without prior consultation with the White House, argued that technical information disclosed at the scientific meetings came under these restrictions. Members of the scientific community, however, have reacted sharply to what many see as an unprecedented attempt by federal authorities to place limits on scientific discourse.

The computer technology meeting was organised in Santa Barbara by the American Vacuum Society to discuss recent developments in bubble memories. A week before the conference was due to open, the organisers received a letter from the Department of Commerce asking them to withdraw invitations extended to scientists in Soviet bloc countries.

Last Monday, just before the conference was due to start, a letter was received from the director of the department's Office of Export Administration stating that "oral exchanges of information in the US with foreign nationals constitute the export of technical data" — and as such required to be licensed.

The Commerce Department subsequently suggested the wording of a pledge, which

all foreigners attending the conference were obliged to sign, stating that they would not reveal any information obtained during the meeting to citizens of the Soviet bloc or other communist countries — including China.

(Three Chinese scientists who had arrived in Santa Barbara for the meeting were also excluded but were admitted on the second day partly, it is believed, as a result of the intervention of the Office of Science and Technology Policy which has been actively engaged in establishing US-Chinese links in science and technology).

The meetings on laser engineering and inertial confinement fusion are being held this week in San Diego, and are jointly organised by the Institute of Electrical and Electronic Engineers and the Optical Society of America.

A Russian post-doctoral student currently studying at the University of Texas, who had had a paper accepted for presentation at the meeting, was subsequently refused permission by the State Department to travel to San Diego to deliver it. On enquiring about this decision, Dr Jarus Quinn, President of the Optical Society, says the State Department told him that several Russian scientists had applied for visas to attend the conference, but that these would be refused.

Commerce Department officials insist that they are merely carrying out the intent of legislation restricting Soviet access to US technology and that the pledges required of participants in the Santa Barbara meeting were necessary to avoid violating technology transfer laws. But the scientists see it differently.

Dr J. Allen Bromley, professor of physics at Yale University and a past chairman of the International Union of Pure and Applied Physics, said that the US action might infringe a position statement issued by the International Committee of Scientific Unions on the behaviour expected of a country hosting international scientific conferences. "If allowed to stand it could damage in a very serious way US participation in international science," he said.

Mr William Carey, Executive Officer in the American Association for the Advancement of Science, commented that the government's actions reflected a "very summary procedure", to interfere so awkwardly in a non-governmental scientific conference.

"It is one situation where the government is managing exchanges carried out under agreements made with another government. It is quite another to interpret a statute and invoke it with no precedent to limit scientific discourse that has been called under private auspices", he said. □

Carter terminates work on nuclear waste disposal project

PRESIDENT Carter has announced the cancellation of the Waste Isolation Pilot Project (WIPP), planned to study the result of depositing high-level nuclear wastes in salt mines near Carlsbad, New Mexico. He argued that to proceed would be inconsistent with the administration's strategy of comparing sites with differing geological characteristics before agreeing to the construction of test disposal facilities.

The President's decision was announced as part of a comprehensive radioactive waste management programme, in which decisions to initiate construction of waste disposal plants are to be put off until further knowledge has been obtained on the behaviour of mined geological repositories capable of accepting waste from both reprocessed and unprocessed commercial spent fuel.

Final decisions on many steps which need to be taken "should be preceded by a full environmental review under the National Environmental Policy Act", the President said. He added that the Department of Energy had already mounted an expanded and diversified programme of geological investigation that recognised the importance of the interaction among geological setting, repository host rock, waste form and other engineered barriers on a site-specific basis.

"Immediate attention will focus on research and development, and on locating and characterising a number of potential repository sites in a variety of different geological environments with diverse rock types", the President said. "When four or five sites have been evaluated and found potentially suitable, one or more will be selected for further development as a licensed full scale repository."

President Carter's decision to terminate the WIPP project, long opposed by environmentalist groups in New Mexico, was also partly based on his desire that all repositories should be licensed. The involvement of civilian licensing bodies had been opposed by defense officials, who would also have used the facility for storing high-level wastes.

As part of his waste storage programme, the President also announced the establishment of a state planning council of elected state, local and tribal officials and heads of cabinet departments and other federal agencies. "The basis of the relationship between states and the federal government in the siting of high level waste repositories will be the principle of consultation and concurrence," the President said. □



United Kingdom

PWRs unlikely to be safe, says metallurgist

CRACKS in the pressure vessels of pressurised water nuclear reactors would be very difficult to detect before they led to catastrophic failure, Sir Alan Cottrell, ex head of the University of Cambridge Department of Metallurgy, told the House of Commons Select Committee on Energy last week. Britain should therefore reverse its decision to build a series of PWRs, and adopt the advanced gas-cooled reactor instead, he argued.

Sir Alan appeared undismayed by the delays in the UK's AGR programme. "They are constructional" he told *Nature*. "The Hinkley Point AGR has performed extremely well." (Hinkley Point, the only AGR in operation, achieved 80% of its design capability in 1979, with an output of over 1000 MW, the Central Electricity Generating Board said this week.)

Sir Alan's first objection to the PWR was that it uses water rather than carbon dioxide as a coolant. "There is a natural safety in CO₂ which H₂O lacks" he says in his written evidence. This is that CO₂ remains gaseous under all reactor conditions, whereas H₂O can exist in two phases — liquid and gaseous — "with very different densities, coolant properties, heat contents, and pressure-volume-temperature relationships".

This leads to two safety disadvantages. First, a PWR must be operated at 150 atmospheres pressure to keep the H₂O liquid at its operating temperature of 320°C; and second "the problems of controlling an irregularity in the operation of a reactor are exacerbated if there is a risk of the coolant suddenly changing its physical state and losing its coolant properties".

The problems which faced the operators at Three Mile Island — "the speed of changes in the reactor, the false indications of the physical state of the coolant, the rapid overheating of the fuel due to the disappearance of the water" — would not have arisen in an AGR "with its lower power density, large mass of heat-absorbing graphite and invariably gaseous CO₂ coolant".

The second objection Sir Alan raised was that it would not be possible to detect a crack in the pressure vessel by the leaking of radioactive material until it was too late.

"To hold the water pressure, the walls of a PWR vessel and circuit have to be thick, up to 14 ins in places, and are made of a fairly hard, strong steel. The thickness and hardness deny the possibility of 'leak before break'. For under these conditions, the critical crack size at which a sharp crack will spread rapidly and uncontrollably is expected normally to be about four inches

but could be as little as one inch under fault conditions. It follows that, if a wall becomes perforated by a growing crack, while under operational pressure, the crack is already unstoppable and will spread to form a major break within a millisecond."

"The security of the reactor thus depends on the avoidance of critically-sized cracks or similar defects in the steel."

Dr Walter Marshall, deputy chairman of the United Kingdom Atomic Energy Authority, had chaired a study of pressure vessel integrity and concluded, according to Sir Alan, that "the assurance of initial safety depends on meeting a number of exacting conditions about standards in workmanship, care in operational control, and rigour in inspection". These conditions, said Sir Alan, "call for considerable human abilities". It was a matter for general judgement "whether this degree of reliance on human abilities provides an adequately sound basis for the safety of a nuclear reactor".

Another worry, said Sir Alan, concerned the possible growth of small cracks, harmless at first, due to metal fatigue and corrosion. If these were discovered (as they have been in some French PWRs) there would remain the problem of repair in reactor conditions.

"The task of developing new equipment to grind out and soundly weld up cracked regions in radioactive steel, remotely by automatic methods, is a formidable one. But if such cracks were allowed to remain and were then to grow large, a government would be faced with a most difficult decision: either to take the chance of running the reactor . . . or to shut-down the reactor at a fraction of its planned economic life."

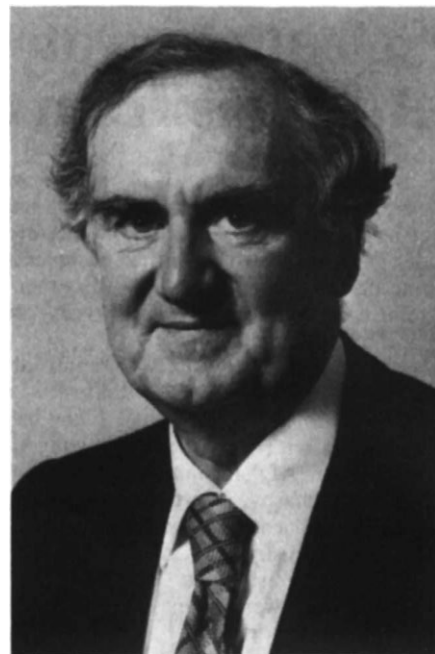
"The long-term value of PWRs may thus depend on the development of a new technology for the remote repairing of thick radioactive steel."

Dr Walter Marshall said on Monday that he accepted the technical basis of Sir Alan's arguments as "correct and completely valid". But "by selecting facts you can give the wrong impression".

For example, on the positive side of water as a coolant is that it is also a moderator — so loss of coolant will also stop the nuclear reaction.

On the "considerable human abilities" required of pressure vessel manufacturers, Dr Marshall said "there are firms abroad that can attain the necessary standards. For example, we could get steel from Japan; and among others Framatome in France and GHH in Dusseldorf could fabricate the vessels."

Was it wise to rely on Framatome, which



Sir Alan Cottrell: doubts about pressure vessel integrity

has discovered cracks in pressure vessels it has built for French reactors? "Well, their big advantage is that they are busy. They may have made one boo-boo but they've learned from it."

"The technology is moving to larger and larger forgings" said Marshall "which you weld together. So ultimately it's the steel manufacturer who matters most. In England River Don in Sheffield could do it."

Dr Marshall does not want to be "sloppy" about inspection. "I want to be able to lay my hand on my heart and say, that one's OK." He would like to have "the full resources" of the UKAEA behind him; the authority itself should be the inspectorate.

If cracks are found, they must be repaired *in situ*, a task which will not be impossible, thinks Marshall. "You would grind out the crack, and not bother to replace the cladding. The water would just get a little rusty." Six specially protected divers successfully replaced the complete reactor support structure under water inside the 'Stada' German reactor in 1973, said Marshall.

Monitoring known cracks, like Framatome's, would not be difficult, but "the most sophisticated, the fundamental question is whether your initial inspection misses any cracks. I couldn't emphasise the importance of the initial inspection too much" said Marshall.

Commenting on Dr Marshall's remarks Dr Cottrell told *Nature* that he feels Dr Marshall has underestimated the repair problems but "we agree on most technical questions; we differ on where we go from there. I take a less cheerful view on whether this rigorous inspection can be achieved. In my view, it's simply asking too much."

Robert Walgate

Hamburg Scientific Forum

No agreement yet over minimising bureaucratic barriers to exchange

INTERNATIONAL scientific exchange must not merely take place; it must be seen publicly to take place. That is how one delegate to the Hamburg Scientific Forum has explained its purpose. The Forum has brought together leading scientists from Europe and North America for two weeks in the service of what has been referred to as the CSCE process, i.e. the implementation of the Helsinki Accords on peace and security in Europe.

The Soviet invasion of Afghanistan and the internal exiling of Academician Andrei Sakharov to Gor'kii mean that the forum is convening among what Dr Armand Boever of Luxembourg calls the "menacing storm cloud of the last few weeks". Inevitably the opening statements by the participating countries delivered last week, put considerable emphasis on the concepts of academic freedom and the responsibility of scientists towards society.

Strong statements on the human rights issue, sometimes citing the Soviet Union by name, sometimes, as did Dr Andre Lwoff (France), referring to breaches of the Helsinki accords in "a certain country", drew an emphatic refusal from the leader of the Soviet delegation, Dr Nikolai Blokhin. "The basic objection is that we observe our laws", he protested, speaking under the

right to reply. "There have been no violations of Soviet law in the Sakharov affair. And Gor'kii is not exile. I myself was born there."

This undertone of confrontation which ran through the entire two and a half days of opening statements, focused attention on the fact that the forum was not, properly speaking, a scientific meeting. When, finally, the preliminary statements were over, and the meeting divided up into working groups on pre-selected topics (alternative energy sources, food production, cardiovascular, tumour and virus diseases, human environment and urban development), the scientists in the various delegations, irrespective of their countries' political system, seemed only too anxious to come to grips with the basic problem of promoting international scientific exchanges.

The majority of western delegates felt that if the forum were to make any real contribution to international exchange — as opposed to simply demonstrating scientific cooperation in the service of detente — it could best do so by endeavouring to eliminate or at least minimise the bureaucratic barriers to such exchange.

Since almost all the 35 delegations

contained a sprinkling of bureaucrats, who sat in on the various working groups, the forum seemed an ideal opportunity for the scientists to make known their grievances against official frustration and obfuscation. This, however, various Soviet delegates were unwilling to allow. Repeated attempts to raise, in the closed working sessions, questions of visas, the cancellation of visits at the last moment for no clear reason, the substitution at conferences of some scientific nonentity for the speaker originally invited, and all the other difficulties and disappointments familiar to the would-be hosts of Soviet scientists, were quashed by the various Soviet representatives. "We are not here to discuss such matters" was their attitude — in which case, one might well ask with Dr Th. P. Tassios (Greece) what unique purpose the forum could serve.

Dr Tassios suggested that a permanent steering committee should be established to "define and shape" scientific "goals" and to deal with the whole problem of the ethics of science. To judge from the opening statements and the general tone of the Forum so far, this is a minority view. Most delegates, at least from outside the socialist bloc, seem to agree with Lord Todd (UK) that whatever the forms of future cooperation to be agreed by the Forum, more organisations to take scientists away from the bench and into the conference jet-set are not needed.

Vera Rich

United Kingdom

Split over admissible evidence at test drilling inquiry

THE UK's first public inquiry into test drilling for the possible disposal of high level radioactive waste got off to a stormy start in Ayr, Scotland last week, with claims that the government was trying to cover up the real issues by restricting the type of evidence. The Scottish office has ruled that it will accept testimony only on the limited question of test site drilling. Community groups, fearing that limited approval for site drilling will create a precedent that will prejudice further hearings, have argued that evidence on the question of the suitability of the area for waste disposal itself ought to be admitted.

The inquiry had been set up to consider a planning application lodged by the United Kingdom Atomic Energy Authority two years ago to test drill an area of hard granite above Loch Doon in the Galloway Hills — possible sites in the UK for Britain's first underground radioactive waste repository. Soon after the planning application was lodged the local authority, Kyle and Carrick District Council, turned it down. The inquiry that opened in Ayr last week is the result of the UKAEA appealing against that decision.

The first witness, Scottish Under

Secretary William Scott, stressed that the government had not yet decided on the best way of disposing of nuclear waste. Research was also planned on waste disposal on and under the sea bed, he said. Under cross examination Scott admitted that he could give no firm undertaking that all the other 15 shortlisted sites would be fully investigated at a cost of £1 million each.

Byron Lintern, a senior scientific officer from the Institute of Geological Sciences, and a witness for the UKAEA, explained that the proposed test drilling would involve sinking approximately 40 boreholes over a wide area at varying depths down to a maximum of 500m. Two 15m rigs would be needed and a staff of about 15. Drilling would be phased over a two or three year period to avoid disturbing local birds during their breeding cycle. The cost of test drilling had risen from £150,000 in 1978 to £450,000 in 1980, he said.

Dr Lewis Roberts for the UKAEA told the inquiry that the UK currently had about 1,000 m³ of high level waste stored in steel tanks at Windscale. It was proposed to glassify the waste, encase it in non-corrosive metal and then find the most

suitable place to store it. A safe home had to be provided for around 500 years, by which time gamma radiation would have decayed to acceptable levels. Roberts rejected Kyle and Carrick's suggestion that the drilling work was "premature."

● ONE of the main objectors at the formal inquiry, the Scottish Conservation Society, organised its own parallel hearing — the People's Planning Inquiry Commission — to discuss nuclear waste dumping, safety and alternative methods of disposal, topics forbidden at the main inquiry. 99% of those attending the 'People's Inquiry' were opposed to the drilling proposals.

The UKAEA declined an invitation to attend, but paid the expenses of Professor John Fremlin, a radiation biologist, who told the meeting that there was little likelihood of the proposed dump causing serious contamination. It would take 100,000 years for the waste to find its way to the surface, he said, and in the worst possible situation would only then result in one death per decade.

Ted Stevens

Ted Stevens is a freelance journalist specialising in planning

The Baltic

States cooperate to check sea pollution

WITHIN the next few days, West Germany, the last of the seven signatories to the Helsinki Convention on the Protection of the Marine Environment of the Baltic Sea area, is expected to deposit its instrument of ratification with the Finnish government. Two months from that day, the convention will come legally into force — the only such agreement to date to cover every aspect of the protection of the marine environment. The delay, caused by federal structure, has not, however, prevented the contracting countries from already embarking on a major programme of work on Baltic ecology.

The Baltic water is of exceptionally low salinity. This results in an ecology of low diversity, which is extremely vulnerable to environmental change. Accordingly, no sooner was the convention drafted in 1974, than a working party, the Interim Commission, was set up to carry out a number of preliminary tasks, including getting to grips with the scientific problems.

Foremost among such tasks is the permanent monitoring of the Baltic for pollution. The convention defines potential pollutants as hazardous (DDT and the PCB and PCT compounds), noxious (heavy metals, radioactive substances, etc) and oil. Seven of these have been selected as immediate priority areas (till 1983), with responsibility for research assigned on the lead country principle: Denmark for PCB and PCT's, West Germany for lead, East Germany for copper and zinc, Poland for DDT, USSR for mercury, Finland for oil, and Sweden for cadmium.

Basic research is not directly the concern of the Commission, although it does serve as a coordinator of the results of the environmental programmes of the individual countries. (Its cumulative bibliography of relevant publications in the Baltic countries since 1970 will be published shortly and there is a proposal to set up an international Baltic library). The main task of the Commission is to work out a coordinated monitoring programme, permitting the direct comparison of results.

A five-year pilot programme was initiated in March 1979. Sampling is to be carried out both at coastal stations and at specified locations at sea. Tests include both the physical monitoring of sea water parameters, and also biological specimens — notably herring, cod, *Macoma baltica*, eider duck, arctic tern and red breasted merganser. To ensure comparability, especially with the biological specimens, a massive file of methodological guidelines, covering all aspects from age and maturity of the specimens selected to test procedures and presentation of results, has been

compiled. This is not yet in its final form, but, according to Dr Ilppo Kaugas, the scientific expert of the Interim Commission, only a very few minor comments and amendments have been proposed.

Intercalibration workshops form an important part of this monitoring programme. To date, these have included a chemical intercalibration workshop at Kiel in 1975 and one on biological calibration methods in 1979. A meeting on biomass, financed by the Commission and organised by Polish marine biologists, will be held in Gdynia in May of this year. In general, Dr Kaugas told *Nature*, the methodology for secondary production is still somewhat vague, and much work may be expected in this field in the future.

The most urgent problem, however, is that of oil spills and ship safety. In the narrow confines of the Baltic, even a close in-shore spill can affect the coasts and waters of other countries. The February 1979 spill of Ventspils harbour (Latvian SSR) ended up on the shores of Sweden and Finland. One recent idea, put forward by a Swedish team, is that all oil cargoes should be "tagged" by the addition of a mixture of metal particles. In the case of a spill, the relative composition of the tagging mixture could be determined by microscopic and mass-spectrographic methods, and this composition, which would be specific to each ship, would, when the convention comes into force, be considered as legal evidence, comparable to a fingerprint.

A large-scale international experiment

on tagging methods was mounted last autumn, investigating such factors as the effect of climatic and meteorological factors on tagged oil. According to Dr Kaugas, the experiments were, in principle, a success, and similar methods "or possibly better" may well be introduced in the future.

Much attention is also being paid to general problems of ship-safety, including the logistics of long-distance pilotage of incoming tankers from the Kattegat to their home ports. One major problem facing the Commission is, however, that of ships sailing under the flags of countries not covered by the convention. "Everything depends in this case on the goodwill of the masters sailing under foreign flags", Dr Kaugas explained. For, although it was at the UN Conference on the Human Environment in Stockholm in 1972 that the Finnish delegation first raised the necessity of international action on the Baltic, and although it is proposed that, when the Permanent Commission is in operation, it will supply data from its monitoring programme to the UN Regional Seas Project, the Helsinki Convention is, essentially, a private agreement between the seven countries bordering the Baltic. The high standard of its monitoring work, and of its anti-pollution proposals (which, once it is signed, will be binding on the participating countries), may well, however, become a blueprint for other future international conventions on marine environments that would cover the whole range of sea-going nations. **Vera Rich**

Women in Helsinki washing carpets in the waters of the port. The seven Baltic states are working to ensure the sea stays clean enough for this spring-cleaning tradition to persist



NEWS IN BRIEF

US urged to spend more on space manufacturing research

UNLESS the US substantially increases the resources that it devotes to research on manufacturing techniques in space, it could see its national pre-eminence in space activities lost to the Soviet Union and Western European countries, according to a report published by the General Accounting Office, the investigative arm of the US Congress.

The report suggests that the federal government develop a plan for broad collaboration with private industry for research into ways of producing substances such as alloys, crystals, semiconductors, and high purity medicines and vaccines in a space environment. Private industry on its own "cannot be expected to risk high, long-term investments at the present stage of research," the GAO says.

The federal government should be spending two to three times the \$20 million currently included in the budget for the National Aeronautics and Space Administration to support such research if it is to retain parity with other industrialised nations, the report says.

Three Mile Island birth defects

OFFICIALS of the Pennsylvania Department of Health confirmed last week that in the last nine months of 1979 13 hypothyroid babies were born in three neighbouring counties compared to an expected number of three such births. The odds against such an event occurring by chance are less than one in 10^5 . Thyroid problems including hypothyroidism are known to be associated with exposure to I^{131} an isotope released into the atmosphere during the Three Mile Island accident. Officials said that likelier explanations than radiation exposure could account for the increase but that the timing was "peculiar and curious".

Supreme Court blow to campus unions

THE US Supreme Court dealt a damaging blow to attempts to unionise university faculty members when it ruled last week that an academic's involvement in managerial and administrative activities made him or her ineligible for collective-bargaining protection under federal labour law.

The Supreme Court's judgement was made on a case brought on behalf of the faculty of the Yeshiva University in New York City, by the National Labour Protection Board, which had argued that nothing in their responsibilities as educators precluded faculty members from

attempting to resolve concerns about the terms and conditions of employment through collective bargaining.

In a five to four decision, the Supreme Court ruled against the NLPB that because universities had to rely on faculty members to participate in making and implementing decisions, for example over course content or the appointment of new faculty members, they were not entitled to the protection offered to industrial workers.

At present, 80 private universities have agreed contracts negotiated through collective bargaining. The court's decision means that in future university officials may be able to refuse to bargain with faculty unions.

French government starts troubled reactors

THE French Minister of Industry, Andre Giraud, authorised last week the start-up of the troubled French reactors, Gravelines I and Tricastin I. Instruments to monitor the growth of cracks 6mm deep and 7-8mm long in the tubular base plates of the primary circuit heat exchanger have been put in place and the ministry considers that the safety of the reactors is assured.

Dutch aerosol propellants ban imminent

DUTCH authorities expect to ban the use of chlorofluorocarbon (CFC) for aerosol propellants from the end of 1981, the Minister of Public Health and Environment, Dr Ginjaar, has said in reaction to reports from the American National Academy of Sciences (*Nature* 3 January, page 2). The member countries of the European Economic Community (EEC) agreed last year to a 30% reduction in propellant use by 1982. Next year the countries will review the position, and if a total ban is not agreed, the Netherlands will do it alone, possibly followed by West Germany.

According to Dr Ginjaar, only these two countries favour more stringent controls. In the Netherlands the use of CFCs as aerosol propellants have decreased by 30% already, and the authorities are now preparing a complete ban on non-essential uses. **Casper Schuurin**

Information withheld on nuclear waste shipments

KEEPING to the government's nuclear information policy of "no news is good news" (*Nature*, 13 December 1979 page 665), the UK Minister of Transport has refused to produce the names of towns and cities through which nuclear waste is regularly transported by rail. Mr Jack Ashley, MP (Labour, Stoke-on-Trent) received a reply to a parliamentary

question from Mr Kenneth Clark, Parliamentary Secretary to the Minister of Transport, stating that the names were being withheld because "it would not be appropriate", to give them. Ashley was told, however, that regular nuclear waste shipments do pass through Stoke-on-Trent.

Nuclear waste transport has been a target for public protest in recent weeks (17 January page 238) causing some official discomfort. At a recent press conference held jointly by the Central Electricity Generating Board and British Rail to explain their position on the shipment of nuclear waste through London, it was revealed that an anti-nuclear campaign plan to stop one of the trains by civil disobedience may have been defeated by information provided by an informer. When asked to elaborate at a later time on the possibility that the CEBG had "its own moles" in the anti-nuclear movement, a CEBG official told *Nature* that the remark was "a light hearted aside" but added that citizens should tell police about wrong doings since "in this country we trust the authorities".

South Africa maintains nuclear weapons capability

A REPORT issued last week* claims that South Africa has developed and maintains a nuclear weapons capability "in order to preserve apartheid in the face of the changing balance of power in southern Africa". Based on a detailed study of South Africa's uranium producing facilities, the report claims that a pilot plant located at Valindaba has the facilities to produce uranium oxide, uranium hexafluoride and enriched uranium. Estimates of plant output since 1975 show that South Africa has accumulated enough enriched uranium to make 4 Hiroshima sized bombs or 12 smaller devices in the 4 kiloton range. Delivery systems would be South Africa's British made Buccaneer and Canberra jets.

In the meantime, confusion exists about responsibility for what is thought to have been a nuclear explosion off the Cape of Good Hope on 22 September 1979. According to information released by the CIA the explosion has been identified from three independent instruments — the radio telescope in Arecibo, Puerto Rico and two independent observations from the Vela spy satellite. The CIA attributes the bomb to South Africa but a book authored by two Israelis published last week claims that the bomb was an Israeli device exploded with South African facilities.

*South Africa's Nuclear Capability by Dan Smith. World Campaign against Military and Nuclear Collaboration with South Africa. 89 Charlotte Street London W1P 2DQ

FEATURES

INFCE brings international agreement on nuclear fuel cycle no nearer

THE International Nuclear Fuel Cycle Evaluation (INFCE) was set up to release growing tension between states over control of the nuclear fuel cycle and the possible spread of nuclear weapons, but, argues **Ian Smart**, without political agreement between governments INFCE alone could not do this

AFTER two and a half years of discussion INFCE has reached its public end with a final plenary session in Vienna. It was bred to be a dispassionate technical analysis of future fuel cycle options in the light of proliferation concerns. How well it has performed will now be tested. Assessments will inevitably vary, if only because different governments looked to INFCE to achieve different things. Especially at the outset, the United States, for example, looked for persuasive evidence that there would be sufficient newly-mined uranium to make reprocessing and the deployment of fast breeder reactors unnecessary for the foreseeable future, and that civil nuclear technology could be developed in 'proliferation-resistant' directions which avoided the presence of separated plutonium.

Others looked for some sort of contrary technical demonstration: that spent fuel would have to be reprocessed to reduce pressure on uranium supply or to make nuclear waste manageable; that plutonium could and should be used in existing thermal reactors; that fast breeder reactors would be needed as quickly as they could be developed; that there were technical means of making any of those activities resistant to proliferation. As the findings of INFCE are studied, it will be found that none of the participants got all it wanted. There is no firm agreement on the future availability of uranium, for example, nor therefore on the rate at which reprocessing should be undertaken or breeder reactors deployed. Indeed, about the only clear conclusions of the technical evaluation are that no conceivable fuel cycle could much reduce the possibility of proliferation and that no single pattern of technical evolution could be appropriate to all national circumstances.

But many of the 46 participating governments have learned something from it on the technical level, and now understand more about the difficulties of both nuclear

fuel cycles and proliferation. One part of INFCE's paradox, however, is that technical experts, dealing with issues many of which were essentially economic, contrived, above all, to achieve a political effect. What they demonstrated, in fact, was that the principal issues raised by a possible relationship between civil nuclear fuel cycles and the proliferation of nuclear weapons cannot be resolved by technical ingenuity or arbitrary government intervention, but only by political negotiation and political agreement.

INFCE can best be regarded as a course of drug therapy, administered to the fevered body of international nuclear energy relations. Partly by that means, the patient's temperature has been reduced. The pathology, however, remains unchanged. The prognosis must therefore be that, the drug having been withdrawn, the temperature will rise again unless the basic disease is identified and treated — and the one thing INFCE has achieved in that connection is to establish that both diagnosis and cure must be political.

The one achievement of INFCE which may, perhaps, be forgotten in a flood of technical commentary is that, simply by meeting for more than two years, it has helped to dissipate the fierce antagonisms that have developed among nations in the nuclear fuel cycle trade.

INFCE arose from international turmoil. At the end of the 1960s, the Non-Proliferation Treaty (NPT) expressed a new international consensus on the need to expand peaceful uses of nuclear energy

without increasing the number of countries controlling nuclear weapons. Provided countries without weapons — non-nuclear-weapon states — substantiated their renunciation of them by permitting international inspection, the treaty acknowledged their right to develop nuclear energy for peaceful purposes without further restriction. The NPT was never universally accepted, but, backed by the safeguards system of the International Atomic Energy Agency (IAEA) and supported by a large majority of governments, it offered some hope of setting the general standard for international behaviour. Five years later, however, both the standard and the hope lay wounded.

In 1974, India, which had not accepted the NPT, tested its first nuclear explosive. Almost simultaneously the Nixon Administration offered power reactors to Egypt and Israel, despite the fact that neither was a party to the NPT. Another nuclear-weapon state, France, having refused to sign the NPT, was negotiating sales of reprocessing technology to both Pakistan (which had also rejected the NPT) and South Korea. West Germany, agreed to provide yet another NPT non-party, Brazil, not only with reprocessing technology but also with equally 'sensitive' equipment for uranium enrichment. And meanwhile the oil crisis was exciting interest in nuclear power and persuading many of those committed to it to seek self-sufficiency.

Shocked by the Indian experience, and fearful that their commercial rivalry, if uncontrolled, might encourage a dangerous increase in the number of countries able to produce weapons, the major governments involved in nuclear exports formed the Nuclear Suppliers Group (NSG) and (secretly) agreed in 1975 on a set of guidelines to govern the export of 'sensitive' items. Although the suppliers eventually published these rules, in 1978, the fact that they had drawn them up in secret and without wider consultation aroused the resentment and apprehension of their customers, especially in the Third World. As to the substance of the NSG guidelines it was soon recognised that they went beyond the NPT itself, by calling for restrictions on the international transfers of certain allegedly 'sensitive' fuel cycle technologies such as enrichment and reprocessing, by limiting the use which those who did import such technology might make of it, and by recommending

'The temperature has been reduced . . . but the pathology remains unchanged'

Ian Smart is an adviser on international energy affairs

that exporters of nuclear fuel should retain the right to veto any reprocessing of it after use.

There was a widespread impression that the guidelines discriminated against the less developed nuclear countries, and that, by implying such countries had no general right to enrich uranium or reprocess spent fuel, even under safeguards, they made nonsense of a fundamental NPT concept. The NPT consensus had been founded on the idea that, for all non-nuclear-weapon parties, all peaceful and safeguarded nuclear activities were equally legitimate. Now it was said that some non-nuclear-weapon states — and some peaceful technologies — were more equal than others.

These resentments were compounded in April 1977, with President Carter's announcement that the US would indefinitely defer reprocessing and the use of plutonium, and would also hold back development of fast reactors capable of 'breeding' plutonium. At the same time, it would withhold approval for foreign reprocessing of US-origin nuclear fuel. Such a policy, subsequently reinforced by the US Congress in the Nuclear Non-Proliferation Act, could be seen as a logical extension of the NSG guidelines. It now struck, however, not only at the transfer of reprocessing (or enrichment) technology but also at the conduct of reprocessing by those who already possessed the capacity: by Britain and France, which had plants, and by West Germany and Japan, which were seeking to build them. The effect was to divide the suppliers against themselves.

The overall result, by the spring of 1977, was that commercial and political confidence in the whole field of international nuclear relations was at a nadir. Contracts had been suspended. Bilateral agreements had been unilaterally recalled, in mid-term, for renegotiation. Multilateral agreements, such as the NPT, had become playthings for minority interpretation. North-South nuclear relations were already embittered, and relations between developed countries were now becoming openly acrimonious. Some cooler review of proliferation issues was urgently needed, if rampant frictions were not to destroy the fabric of international cooperation and trade.

So INFCE was conceived at the May 1977 Economic Summit in London, and officially born in October of that year in Washington. Its eight working groups,

'As the findings of INFCE are studied, it will be found that none of the participants got all they wanted'

with the Technical Co-ordinating Committee (TCC) composed of their 22 co-chairmen, have since held 70 meetings and produced 20,000 pages of commentaries and drafts. Now it is winding up, with a final plenary session whose task this week is to set its seal on the lengthy 'Overview' agreed in the TCC and on the even longer reports of the separate working groups. And next come the consequences of its three years' work.

In the short term, international nuclear relations will inevitably come under renewed pressure. In several countries — Sweden and West Germany, for instance — the link between nuclear power and proliferation is an immediate issue in domestic politics. In several cases, as between the United States and Japan or the United States and Euratom, bilateral arrangements for nuclear cooperation and trade must now be re-cast in more restrictive form. And in August 1980, at the multilateral level, parties to the NPT must meet at their second Review Conference, where the political tensions unresolved by INFCE will again be prominent. Unless those and other immediate stresses are successfully absorbed, the temperature of international nuclear relations could easily be rising again by the end of the year.

Looking to the longer term, the problem is simpler but more difficult. What has collapsed since 1974 is not some set of formal rules or standards but rather the sense of international confidence: confidence that nuclear power can be used more widely without intolerably increasing the risk or fear of weapons proliferation; confidence that international contracts and agreements will be fulfilled, and that all those who seek the energy benefits of nuclear power will be able to draw equitably on international trade under safeguards.

As a result, nothing less than the world pattern of nuclear energy development is at stake. On one side, there is a model of development in which countries committed to nuclear energy programmes, but unconvinced that essential goods and services will always be available on acceptable terms, are driven to seek nuclear autarky as the only other route to energy security. With little regard to cost, more of them will then for instance, acquire their own plants for enrichment and reprocessing.

On the other side is a model of inter-dependent development, in which the same countries, offered a reliable system of nuclear trade and cooperation, will voluntarily optimise their programmes within a regional or global context. Political and economic rationality will then coincide to produce an efficient international distribution of labour in the nuclear fuel cycle, including its 'sensitive' stages.

The former pattern of 'fragmented autarky' would clearly generate greater fears of proliferation, while also being resistant to internationally agreed regulation or safeguarding. The paradox of some supplier policies since 1974, however, is that, by seeking to restrict nuclear trade and confine fuel cycle technology and capacity to a few countries in the name of non-proliferation, they have reduced the confidence of other states in inter-dependent development and actually increased the pressure on them to move to 'fragmented autarky', making the system progressively less amenable to international regulation.

The privately sponsored International Consultative Group on Nuclear Energy, in its recent report, has called for "a new 'bargain of confidence', in which credible guarantees of peaceful purpose will be balanced by firm assurances of access to nuclear services, materials and technology". Such a bargain of confidence can only be achieved by political negotiation. Non-proliferation treaties and international safeguards provide a starting point, and INFCE may offer some signposts. Experience of the last decade proves, however, that more is needed: some general code of conduct for international nuclear trade, agreed by importers as well as exporters, and possibly some more imaginative institutional arrangements for the international management of 'sensitive' activities and materials.

The alternative is not to be contemplated. Ten years ago, governments made the mistake of turning away from the NPT before its general provisions had been converted into concrete and equitable arrangements suited to specific international circumstances. INFCE has solved nothing, but it has bought an opportunity to repair some part of that gross error. If governments, especially in the advanced nuclear countries, fail to build onwards from INFCE into a lattice of political negotiation, design and agreement, they will have only themselves to blame if, in another few years, international nuclear relations are again as inflamed and painful as they were when it started. □

In Nature next week Sir Hermann Bondi, chief scientist at the UK Department of Energy and leader of the UK delegation to INFCE over the past two years, explains how INFCE reached its technical conclusions.

'Nothing less than the world pattern of nuclear energy development is at stake'

CORRESPONDENCE

Iraq's efforts to reverse the brain drain

SIR, — I was very pleased with Ziauddin Sardar's article in *Nature* (January 24, page 327) in which the author goes into depth in an effort to describe the exporter and importer countries of scientists and the problems these scientists face in the host countries. Although the report reflects the realities in these countries, it failed to mention anything about Iraq, a country that has a very clear policy in attracting expatriate scientists to return and establish residence in Iraq. In fact as early as 1974, the Revolutionary Command Council of Iraq instituted the "law of return" to any Arab scientist, engineer or holder of a high university degree to return to Iraq. The government, on its part, provided the returning scientists with several enticements including:

- all the facilities needed to do science
- an option to acquire the Iraqi citizenship after a year's stay
- a lot of land to build a house
- a substantial, long term, interest-free loan to effect the building of the dwelling.

Iraq's ambitions to foster science and technology is evident by the construction of new universities and science centres, in recent years, to accommodate the returning scientists as well as to accommodate the ever-increasing number of graduates sent to various developing countries for higher studies and training.

The development of science and technology receives support at the highest levels. Indeed Mr Saddam Hussain, the President of Iraq, gave his clear instructions to do what it takes to develop the scientific base in Iraq. He personally authorised the establishment of a new programme of short-term training seminars to be held in Iraq at government expense. The trainees are Iraqi and other Arab nationals and the training staff are scientists residing in the western world. I personally, along with my colleagues of the Arab American University Graduates (AAUG) had the opportunity to conduct some of these seminars in Baghdad, under the auspices of the Ministry of Health.

Because of its pan Arab nationalistic policy, the government of Iraq insists that "Iraq is for Arabs". This policy is translated into action by waiving the visa requirements to any Arab national, wherever he lives, and who wishes to visit, work or establish a home in Iraq. To my knowledge this is the only Arab country that has felt secure and abolished the visa requirements. To further promote the feeling that Iraq is for Arabs, the non-Iraqi Arab nationals are treated as equal to their Iraqi counterparts. The treatment of "second class citizens" of the expatriates mentioned in Sardar's article is non-existent in Iraq. One can safely deduct that Iraq's long-term ambitions are to bring Baghdad to its golden days as a centre of science and technology.

I am neither an Iraqi national nor a member of the ruling political party, but a concerned Arab scientist residing in the United States and currently on short leave in Switzerland.

ABDALLAH M. ISA

Institut für Klinische Immunologie, Bern, Switzerland

Defending democracy or something else?

SIR, — Your correspondent (Rolf Seifert, 31 January, page 426) alludes to the "suicide of democracy" if "disruptive Marxists" are allowed to occupy "influential positions" in society. According to cases we are actually involved with, "influential positions" include postmen, railwaymen, teachers of educationally subnormal children and civilian army cooks as well as the cases quoted in *Nature* (6 December, page 549).

It is the suicide of democracy for the state to monitor legal involvement in the democratic process, to label them arbitrarily as 'disruptive', and then continue to use them as a criteria for the dismissal of long-standing public employees from their jobs. When you defend democracy by such methods, you do not defend democracy, you defend something else.

There is an old English proverb about killing the goose that lays the golden eggs.

C. N. M. POUNDER

National Campaign against the Berufsverbote, Edinburgh, UK

Nuclear safety conference open to the press

SIR, — In "News in Brief" (24 January, page 326) you mention the IAEA's International Conference on Current Nuclear Power Plant Safety Issues, to be held in Stockholm from 20-24 October 1980, with a misleading title. I would like to make the following points:

- This conference, like all others organised by the Agency, is open to the press and to the public, accommodation in the conference hall permitting.
- The requirement that papers be submitted by governmental designees is a standard requirement for all meetings of the United Nations and its agencies, since they are inter-governmental bodies, and in practice, therefore, these papers represent a wide range of opinions.

GEORGES DELCOIGNE

International Atomic Energy Agency, Vienna, Austria

Makerere University library appeal

SIR, — We would like to bring attention to some of the difficulties currently being faced by Makerere University in Uganda, particularly with regard to the university's library. All finance for the library was cut off in 1974, and in the last few months since the liberation only a portion of it has been restored. In consequence all runs of the 2000 or so learned journals which the library used to take ceased, as did the purchase of new books. Moreover during the recent fighting many books and much library equipment were looted.

A university cannot function effectively without a good up-to-date library, and teaching and research must both be severely hampered. Makerere used to have one of the best libraries in East Africa, housed in a beautiful building, and both of us have in the past spent many peaceful hours working in it. We have therefore decided to open a fund to

help re-equip the library, and we appeal to all those with an interest in Makerere and a concern for education in Africa to contribute generously. We will ensure that the fund is used for the designated purpose by consulting with the librarian and then purchasing and despatching books to him. If you would like to help please send a cheque made payable to the "Makerere Library Fund" to one of us at the address below.

PATRICK MANGHENI
PETER MILLER

The Queens College, Oxford, UK

Maoist dogma clashes with fair appraisal of science

SIR, — I deplore the descent of *Nature* into the murky realms of propaganda. A series of feature articles on Chinese science by Tong B. Tang published in the 31 January, 7 February and 14 February issues use the most blatant political jargon, something totally unsuited to a scientific periodical. The epithet 'Gang of Four', a political insult which would not be out of place of George Orwell's book *1984*, 'revisionism', 'capitalist roaders' and other jargon, combined with Maoist unintelligibles like "one divides into two" combine to make the articles unpalatable. Surely the peculiar outpourings of Maoist dogma clash with a fair and dispassionate appraisal of progress in Chinese science. The 'ascent of deviationists' may be of interest to the changing policies of Marxist doctrinal quibblers, but such extravagant phraseology masks what is really the issue — the use of science for political ends. Like so-called Islamic science or even Christian science, these 'sciences' which are oriented to some prearranged goal like the 'dialectics of nature' serve only to bolster the preconceptions and prejudices of dogmatic plutocrats.

NIGEL PENNICK

Cambridge, UK

Critic of "The Sirius Mystery"

SIR, — Robert K. G. Temple's long letter (17 January, page 242) seems to have been, in part, motivated by a sense of indignation at not having been appropriately cited by Rowan Robinson (in his review of Carl Sagan's "Broca's Brain", (8 November, page 176) nor by Carl Sagan (in his book "Broca's Brain").

It is therefore worth pointing out that Temple himself carefully avoids any reference to articles critical of the claims he makes in his book "The Sirius Mystery." One such article that readers of *Nature* might wish to know about is Pesch, P. and Pesch, R. *The Observatory*, 97, 26; 1977.

PETER PESCH

Warner and Swasey Observatory, East Cleveland, Ohio, US

Radical test

SIR, — With reference to the Shirley Williams interview (3 January, page 8), it is odd she should choose herself as "litmus paper" while her colleague, Mr Prentice, so readily changed from red to blue. It seems he failed the acid test of being a radical.

D. P. HAWORTH

Department of Botany, University of Illinois, US

NEWS AND VIEWS

Transposable mating-type genes in yeasts

from Urs Leupold

THE genetic analysis of the inheritance of yeast mating types has developed recently from a rather specialised subject studied by only a small group of yeast geneticists into one of central genetic interest. This is due to the growing realisation that the mating type switches observed in both *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* are yet another example of the phenomenon of transposable or translocatable genes whose importance is increasingly being recognised throughout the living kingdom.

Saccharomyces cerevisiae

In *Saccharomyces cerevisiae* there are two mating types a and α . Vegetative haploid cells of opposite mating type can fuse to form vegetative diploids which may subsequently sporulate, producing haploid spores. In homothallic strains of *S. cerevisiae* haploid cells of one mating type can 'switch' mating type during vegetative growth, giving rise to progeny of the opposite mating type.

In *S. cerevisiae*, the results of the genetical analysis of mating-type interconversions in homothallic and heterothallic strains have led I. Herskowitz and coworkers to develop a hypothesis known as the 'cassette model' to explain the observed interconversions (reviewed by I. Herskowitz *et al.* in *The Molecular Genetics of Development*, ed. Loomis, W. & Leighton, T., Academic Press, 1979). Briefly, this model proposes that the switching between the two opposite mating types a and α ; which occurs as frequently as every cell division in homothallic strains, is due to the transposition of α and a alleles from silent storage sites to the mating-type locus where they replace the allele present, either a or α . The storage sites carrying either an a or an α allele in an unexpressed

form have been characterised genetically as two gene loci *HML* (carrying the α or, less frequently, the a allele) and *HMR* (carrying the a or, less frequently, the α allele). The two loci map far from the mating-type locus *MAT* but in the same chromosome on opposite sides of *MAT* (*HML* in the left and *HMR* in the right arm) (see Fig. 1). In the presence of the *HO* gene for homothallism which allows for frequent switching (as opposed to the rare mating-type interconversions observed in heterothallic strains of constitution *ho MATa* and *ho MATa*), defective mutant alleles of the type *mata*⁻ or *mata*⁻ are quickly replaced by the corresponding functional alleles which are stored in a silent form at the *HML* and *HMR* loci. Mutations induced in the *HML* and *HMR* loci can also be transposed to the *MAT* locus by switching. This transposition is a long-range transfer and seems to occur also in the *trans* configuration between different (homologous) chromosomes.

A recent paper by J. Hicks, J.N. Strathern and A.J.S. Klar (*Nature* 282, 478; 1979) offers physical evidence for the existence of homologous sequences at the *MAT*, *HML* and *HMR* loci which is entirely consistent with the cassette model. Moreover, it shows that this homology is not restricted to alleles which determine the same mating type (for example *MATa*, *HMLa*, *HMRa*) but that even alleles determining opposite mating types (for example *MATa*, *MATa*) share homologous sequences. DNA restriction fragments carrying an α allele of either *MAT*, *HML* or *HMR* differ however from restriction fragments carrying a alleles in being uniformly about 200 base pairs larger. Both homothallic (that is, frequent) and heterothallic (rare) mating-type interconversions involve a corresponding change in size of the restriction fragment carrying *MAT*. This shows that the

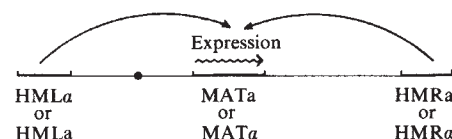


Fig.1. Relative arrangements of *HML*, *MAT* and *HMR* on chromosome III of *S. cerevisiae*. During mating type interconversion a copy of a or α is inserted into the *MAT* locus where it is expressed. The sequence previously located at the *MAT* locus does not reappear in the genome and is presumably lost. (After Hicks *et al.* *Nature* *op. cit.*)

interconversion process involves a rearrangement of the DNA sequences present at the *MAT* locus, most probably the substitution of an a or α sequence by a partially homologous α or a sequence from one of the silent genes *HML* or *HMR* as predicted by the cassette model.

These remarkable results have been obtained by cloning a 6.6 kb *Bam*HI restriction fragment carrying an α allele sequence (the *HMLa* allele) on a plasmid capable of replicating in both yeast and *E. coli* and of transforming yeast at high frequency. The cloned sequence was identified by its ability to complement a defective *mat* allele for both mating and sporulation when plasmid DNA carrying the α sequence was introduced into cells carrying the mutant allele at the *MAT* locus. When this plasmid was used as a hybridisation probe against Southern blots of restricted DNA from a series of different yeast strains carrying known mating-type alleles at the mating-type locus *MAT* and the two silent loci *HML* and *HMT*, characteristic differences in restriction patterns between a and α strains were observed. In tetrad analyses of meiotic crosses between strains differing in their mating-type constitution at either the

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mating-type locus or one of the silent loci, these differences segregated along with the mating-type alleles studied.

Klar, Hicks, Strathern and J. Broach have presented these results at a meeting on the Molecular Biology of Yeast which took place in Cold Spring Harbor last year. There they presented additional evidence (not mentioned in the paper) based on heteroduplex mapping which shows that the α allele differs from the a allele not only in the addition of a sequence of about 200 base pairs but also in the substitution of an adjoining sequence of about 700 base pairs. The heterologous region (700 bp in a and 900 bp in α) is flanked on both sides by homologous regions which permit hybridisation between complementary a and α strands.

These findings have independently been confirmed and extended by K.A. Nasmyth and K. Tatchell who have cloned the α sequence from the *MAT* locus and who have also discussed the results of a heteroduplex analysis of the three mating-type genes at the same meeting. A paper presenting their data will shortly be published (*Cell*, in press). A heteroduplex analysis of the six possible combinations between purified *Hind* III fragments carrying *MAT α* , *MAT a* , *HML α* or *HMR a* showed that the homologous regions common to all loci are confined to two blocks of DNA, one of 230 base pairs located on one side (the 'left' side) and one of 700 base pairs located on the opposite side (the 'right' side) of the a/α specific sequence of approximately 800 base pairs (700 bp in a and 850 bp in α according to their data). The a and α specific insertions are present in the same orientation, with respect to the two homology blocks, in active and silent loci. *HMR a* lacks an extensive 700 bp DNA sequence to the right of the large right hand homology block and probably also a small (100 bp) sequence to the left of the small left hand homology block, both of which are present at *MAT* and *HML α* (see Fig. 2). In *MAT a* and *MAT α* , the regions of homology flanking the a/α specific sequence extend to the ends of the 4.1 kb and 4.3 kb *Hind* III fragments carrying the a and α alleles of the *MAT* locus.

On the basis of these data, the extent of the sequence transposed from *HMR a* to *MAT α* in an $\alpha \rightarrow a$ switch seems to be at least 700 bp and at most $230 + 700 + 700 = 1,630$ bp. In an $a \rightarrow \alpha$ switch, the sequence transposed from *HML α* to *MAT a* consists of a minimum of 850 bp but may include as many as $100 + 230 + 850 + 700 + 700 = 2,580$ bp. The extensive sequence homology shared by the active mating-type locus *MAT* and the silent loci *HML* and *HMR* suggests that the interconversion replacing the resident mating-type sequence at the *MAT* locus by an alternative sequence from one of the two silent genes may occur by a mechanism of non-reciprocal gene conversion. This would involve an intrachromosomal

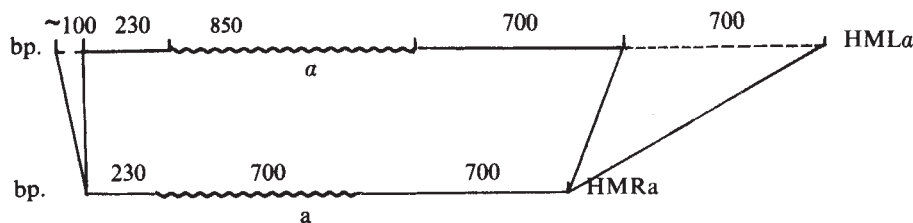


Fig. 2. Schematic representation of the differences between *HML α* and *HMR a* (see text for explanation).

alignment of active and silent loci of opposite type, followed by the transfer of a single-strand DNA segment from the silent to the active locus where it replaces the corresponding segment including the central sequence of opposite mating-type specificity. The resulting heteroduplex structure containing an unpaired loop in the centre of the *MAT* locus could then be resolved either by local excision repair which replaces a DNA segment of the resident *MAT a* or *MAT α* strand by a complementary copy of the transferred *HML α* or *HMR a* single-strand segment, or by normal DNA replication with leads to the segregation of two daughter chromosomes carrying alleles of opposite mating-type specificity at the active mating-type locus. The recent finding of R.E. Malone and R.E. Esposito (also reported at the Cold Spring Harbor yeast meeting mentioned above and see *Proc. natn. Acad. Sci. U.S.A.* 77, 503; 1980) that a DNA repair mutant defective in both meiotic and mitotic recombination (*rad52-1*) prevents homothallic switching, lends direct support for the involvement of generalised recombination functions in the mating-type interconversions observed in yeast.

Together, the two reports from the groups of J. Hicks and coworkers in Cold Spring Harbor and of K.A. Nasmyth and K. Tatchell in Seattle represent the first physical evidence confirming the genetical evidence that the two silent mating-type loci *HML* and *HMR* show an extended sequence homology with the active mating-type locus *MAT* and with one another when carrying alleles of the same mating-type specificity, either a or α . They demonstrate further that even when carrying alleles of opposite mating-type specificity, the three loci share homologous sequences although their a and α alleles differ in a central region of 700 and 850 base pairs, respectively. Together with the genetical evidence obtained by the group of I. Herskowitz at the University of Oregon and by many others, they provide very strong support for the cassette model which proposes that the mating-type interconversions in yeast are due to the transposition of mating-type alleles from silent storage sites ('cassettes') to the mating-type locus where they become expressed.

The mating-type locus plays a key part in the differentiation of yeast cell types for it controls not only mating but also sporulation. Diploid cells homozygous for the a or α allele at the mating-type locus *MAT* can mate with cells of the opposite mating type but are unable to undergo meiosis and sporulation. Diploid cells of heterozygous constitution *MAT a /MAT α* can be induced to undergo meiosis and sporulation but are unable to mate with either a or α cells. An understanding of the role of gene transposition in the differentiation of these yeast cell types may well contribute to a future understanding of cell differentiation in higher eukaryotes (see I. Herskowitz *et al. op. cit.* 1979).

Schizosaccharomyces pombe

Mating-type switching in *Schizosaccharomyces pombe* (see Egel *Nature* 266, 172; 1977), although still in the purely genetic phase of research, has recently been shown to resemble 'cassette-recording' in *Saccharomyces*, partially at least (R. Egel, Copenhagen, as presented at the Cold Spring Harbor meeting). One of the two closely linked mating-type genes found in this species, *mat2-P*, has turned out to represent the silent store of 'plus' information, which can only be activated by copy-transposition to *mat1* — the 'mating-type locus'. The 'minus' information residing at *mat1-M* beforehand is formally replaced by the inserted *P* copy, but whether this is merely due to transient separation of *M* from its controlling signal or whether the *M* segment is, in turn, excised is still unknown. In the latter case another gene of silent *M* storage should exist elsewhere, for which there is as yet no evidence. A major difference remaining (relative to *Saccharomyces*) lies in the fact that this *P* transposition requires the close linkage here encountered and does not function in the *trans* configuration. This linkage and the *cis* effect have hitherto obscured the activation mechanism of the *P* gene, which only revealed itself after mutants had become available that reduce the naturally high frequency of switching. In such mutants the activated (transposed) *P* copy remained in place long enough to be detected. Otherwise it was lost too soon (within 1-3 cell divisions) by the next switch-back reaction. □

Interstellar grains in meteorites?

from R. Hutchison

TODAY, the most favoured theory of the origin of the Solar System entails the collapse of a gas-dust cloud, perhaps initiated by a shock-wave from a nearby supernova. Heating during the collapse phase would have vaporised much, if not all, of the pre-existing dust. The question then arises: did any of the presolar dust-grains survive? And if so, how might they be recognised? Answers to these questions may be found in carbonaceous chondrite meteorites.

Evidence that some materials are enriched in the products of a supernova (or supernovae) was found in inclusions in the Allende meteorite. The scientific community was extremely lucky to receive two tonnes of specimens from the Allende meteorite shower that fell in northern Mexico in February, 1969, making available for study kilograms of samples of a type which had previously been doled out in gram-sized amounts. The Allende material was found to contain whitish inclusions consisting of minerals rich in calcium, aluminium and titanium. Such mineral assemblages were soon recognised as those predicted by Lord in 1965 (*Icarus* 4, 279) as the first material to condense from a cooling gas of solar composition. And in 1973, R.N. Clayton *et al.* (*Science* 182, 485) established that the oxygen of the high temperature inclusions and chondrules of Allende and related carbonaceous chondrites is enriched in pure ^{16}O . It was argued that the pure ^{16}O was produced by nuclear processes in an expanding outer shell of a supernova. Soon after the pure ^{16}O was introduced into the Solar System, condensation of refractory minerals trapped a portion of the pure isotope, the remainder having been mixed in with average Solar System oxygen, so losing its identity.

Further studies revealed that the white, calcium, aluminium, titanium-rich inclusions of Allende have anomalous isotopic abundances of various elements. Potentially, the most important of these anomalies is in ^{26}Mg because this is the daughter isotope of ^{26}Al , of which the half-life is only 740,000 years. The ^{26}Mg anomaly was discovered by Gray and Compston (*Nature* 251, 495; 1974) and by Lee and Papanastassiou (*Geophys. Res. Lett.* 1, 227; 1974). Wasserburg's group soon showed that in several Allende inclusions there is an internal isochron relationship between $^{26}\text{Mg}/^{24}\text{Mg}$ and $^{27}\text{Al}/^{24}\text{Mg}$ (*Geophys. Res. Lett.* 3, 109; 1976). The isotope ^{27}Al is the only stable isotope of the element, and ^{24}Mg is the most abundant common isotope of magnesium. Thus, in each mineral of some inclusions there is a positive correlation between ^{26}Mg and the aluminium to magnesium ratio. We can therefore

conclude that these inclusions crystallised when ^{26}Al was still extant. But, as D.D. Clayton has pointed out, there is no positive proof that the white inclusions crystallised within the Solar System (see for example *Nature* 257, 36; 1975). Because isotopic anomalies of different elements, but especially light and heavy elements, do not generally correlate with each other, it is argued that crystallisation of the white inclusions must predate the Solar System. Injection of newly synthesised nuclides from a supernova into a presolar gas-dust cloud should have caused complete mixing of the injected elements. Thus, any isotopic anomalies should be correlated within each white inclusion. Lack of such correlation may be interpreted as indicating that the white inclusions represent condensates from the outer shells of the expanding supernova itself, assuming that the shells are blown concentrically outwards with a minimum of mixing between them.

Last year, a presolar age for two Allende inclusions was given a boost. Jessberger and Dominik (*Nature* 277, 554; 1979) found that two inclusions have ^{39}Ar - ^{40}Ar ages of about 5.0 Ga. The technique uses the ^{40}K - ^{40}Ar decay scheme, but ^{40}K is estimated from the amount of ^{39}Ar produced by neutron irradiation of ^{39}K . If the $^{40}\text{K}/^{39}\text{K}$ ratio throughout the inclusion had been uniformly high, it could have accounted for the apparently old age. However, Stegmann and Begemann (*Nature* 282, 290; 1979) found the potassium isotopic ratios to be normal. Thus the inclusions seem to have crystallised 400 Ma before the birth of the Solar System. But because other age determination techniques give a 'normal' age of about 4.55 Ga for Allende and its inclusions (see for example Tatsumoto *et al. Geochim. cosmochim. Acta* 40, 617; 1976 and Chen and Tilton, *ibid.*), the ^{39}Ar - ^{40}Ar age is still treated with suspicion. Even so, there seems to be a good chance that in some of the Allende inclusions we have presolar aggregates of refractory minerals up to about 1 cm in diameter.

Other approaches in the search for presolar, interstellar grains have been taken by Anders' group at Chicago and Eberhardt's at Bern. In 1969, Black and Pepin argued by a process of elimination that an anomalous neon component in some meteorites is of presolar origin (*Earth planet. Sci. Lett.*, 6, 395; 1969). This type of neon, 'Ne-E', is characterised by low $^{20}\text{Ne}/^{22}\text{Ne}$ and $^{21}\text{Ne}/^{22}\text{Ne}$ ratios; Ne-E is, therefore, highly enriched in ^{22}Ne . Because noble gases are released from mineral grains at moderate temperatures, any carrier of Ne-E could not have had a high temperature history like that of the Allende inclusions. So, if the carrier minerals of Ne-E could be separated and identified, this

might provide a sample of interstellar grains. To this end the Chicago group used chemical separation techniques and the Bern group physical methods.

Lewis *et al.* of Chicago (*Astrophys. J. Lett.* 234, 165; 1979) used a sample of the water-bearing, CM2, carbonaceous chondrite which fell at Murchison, Victoria, Australia in September, 1969. As with Allende, scientists were fortunate to have been provided with about 500 kg of a type of meteorite which had previously been in short supply. The Chicago group dissolved away over 99.7% of their sample, using various reagents including HF, HNO₃, NaOH and H₂O₂. The residue was split into three size-fractions and from aliquots of each the rare gases were extracted by stepwise heating. Isotopic ratios were measured in the gas released at each heating step. Ne-E was released from the coarse (>3 μm) fraction in two steps at 800 °C and 1,200 °C. Low-temperature (800 °C) release was not observed in an aliquot of material which had been treated with HClO₄. The low temperature carrier destroyed by HClO₄ was thought to be an oxidisable, carbon-rich material. From previous work and from its resistance to attack, the high temperature carrier of Ne-E was tentatively identified as spinel (MgAl₂O₄). In addition to carriers of Ne-E, a carrier of s-process xenon was identified as a carbon-rich phase stable at 1,400 °C. Lewis *et al.* concluded that the two carbonaceous phases and spinel are 'extrasolar'. However, stability of spinel requires a more oxidising environment than phases rich in elemental carbon. The authors, therefore, speculated that the extrasolar minerals may be condensates from red giants "at different stages of evolution".

The Bern group prepared nine density fractions of the Orgueil, water-bearing, carbonaceous chondrite, and stepwise heating was used on all but one, which was too small (*Astrophys. J. Lett.* 834, 169; 1979). Ne-E was most highly concentrated in the least dense fraction (<2.3 g cm⁻³), from which it was released below 900 °C. From three high density fractions (total range, 2.9-3.6 g cm⁻³) Ne-E was mostly released at about 1,200 °C. Because potential contaminants are of lower density, it was argued that the Ne-E carrier probably has a density of about 3.5 and is probably spinel. Eberhardt *et al.* point out that the low density fraction has a low content of cosmic ray-produced ^{21}Ne , which indicates a low abundance of the target elements Mg, Al and Si, and is consistent with a carbon-rich composition. Furthermore, the composition argues against the possibility of the *in situ* production of pure ^{22}Ne by particle bombardment within the Solar System. A presolar origin of one Ne-E carrier therefore seems assured. □

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The hard X-ray Sun in stereo

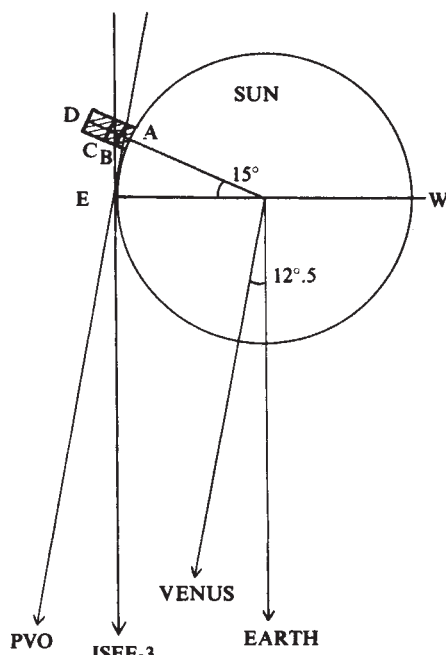
from John C. Brown

VIRTUALLY on the eve of launch (14 February, 1980) of the first ever solar hard X-ray imaging telescope, aboard NASA's Solar Maximum Mission (SMM), a group of US researchers has scooped some of its expected results without the use of imaging instruments. Kane and Anderson of Berkeley and Evans, Klebesadel and Laros of Los Alamos (*Astrophys. J. Lett.* **233**, L151; 1979) have obtained quantitative information on the spatial structure of a solar hard X-ray source by simultaneous observations from two separate spacecraft. Their results provide invaluable insight into the process of electron acceleration which is central to the solar flare problem.

At the time of observation (5 October, 1978 around 0632 UT) an International Sun Earth Explorer (ISEE-3) was located near the Earth while Pioneer Venus Orbiter (PVO) was 12.5 degrees eastward as seen from the Sun (see Figure). Fortunately, a flare occurred in an active region A some 15 degrees behind the solar limb which consequently occulted different parts of the flaring solar atmosphere from the two spacecraft. As a result (see Figure) ISEE-3 observed only X rays emanating from altitude (C-D) in the source greater than 25,000 km above the photosphere (A) while PVO observed all emissions (B-D) from above 700 km altitude. At burst peak the PVO flux above 50 keV photon energy exceeded the ISEE flux, extrapolated to the same energy range, by a factor of 600 and had a spectrum harder by about +2 in the power-law exponent. We can thus conclude that the hard X-ray source is concentrated at altitudes below 25,000 km, particularly at higher photon energies, with a factor of 600 above 50 keV. This result is a great advance on previous behind-the-limb results from single spacecraft which established the existence of a high altitude source component but gave no information on the differential height structure.

The importance of hard X-ray bursts lies not in the bremsstrahlung X rays themselves but in the energy of the electrons emitting them. These electrons represent a significant, and perhaps a large, fraction of the total energy released by magnetic field dissipation in a solar flare. How severe are the demands that this places on the electron acceleration process depends strongly on the hard X-ray source model assumed. In particular the acceleration efficiency involved is modest if the bulk of the source electrons are in a relaxed quasi-thermal state. On the other hand, if the source electrons are non-thermal they lose most of their energy by collisions to the cooler thermal plasma rather than to bremsstrahlung and a far greater total electron energy is required.

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Schematic showing directions of the two spacecraft as seen from the Sun and the different heights in the X-ray source (hatched area) seen from each spacecraft.

Two possible cases of the latter situation are the descending electron beam (thick target) model (with acceleration near D in the Figure) and the trap model where fast electrons are confined in a magnetic arch after acceleration. Although these latter models pose problems for acceleration mechanisms, they provide a plausible interpretation of impulsive chromospheric emissions in flares in terms of electron bombardment. The greatest single source of ambiguity in modelling hard X-ray bursts to date has been the lack of spatial resolution.

There seems to be no ready interpretation of Kane *et al.*'s results in terms of the trap model since this predicts comparable X-ray fluxes from the trapped (coronal) electrons and those precipitating down the limbs to the chromosphere (unless by chance ISEE just glimpsed part of the arch summit at C). A thermal model just might fit the facts if quasi-thermal emission emanated from CD at energies up to around 50 keV while the high energy electron tail escaped downward. The most convincing interpretation at present, however, is the thick target model which predicts a difference of +2 in spectral index between coronal and chromospheric components, and much greater total flux at low altitudes (Brown & McClymont *Solar Phys.* **41**, 135; 1975). The PVO/ISEE flux ratio would then require an acceleration site D located at a plasma column depth of 2.5×10^{18} protons cm^{-2} above the 25,000 km level C. For quiet Sun conditions the plasma density n here is around 10^8 cm^{-2} , but such a low density could not sustain a

stable reverse current to neutralise the descending beam. Reverse current stability demands $n \geq 5 \times 10^9 \text{ cm}^{-3}$ which is consistent with the density enhancements typical of active regions. It will be of great interest to see whether a similar source distribution with height occurs in other bursts or if these are more consistent with one of the other source models.

In the coming months SMM will disgorge vastly more hard X-ray source spatial data than are contained in Kane *et al.*'s results. Specifically it will yield detailed information on horizontal source structure and so test whether electrons really do bombard the chromosphere. On the other hand the SMM telescope is limited to photon energies below 30 keV and, furthermore, has no spatial resolution along the line of sight. Thus the 'stereo' data of Kane *et al.* will remain unique until we are again fortunate enough to have two spacecraft and a flare in the right places at the right time. □

Tailoring liposome structure

from Gregory Gregoriadis

THE idea that drugs entrapped in lipid envelopes (liposomes) may provide a better means of delivery to specific sites within the body has aroused wide interest. Much of the interest in the liposomal carriers has no doubt stemmed from the almost unlimited number of potential versions in terms of composition, size and other characteristics. Indeed, correct choice of these parameters has, in some instances, led to liposomal preparations best suited for optimal drug action (for reviews of various aspects of liposomes see *Liposomes and their uses in Biology and Medicine* (D. Papahadjopoulos ed.) *Ann. N.Y. Acad. Sci.* **308**, 1978; *Liposomes in Biological Systems* (eds G. Gregoriadis & A.C. Allison) John Wiley and Sons Ltd, 1980). Recently, attempts have been made to rationalise liposome development by tailoring their structure to the particular biological milieu in which they are intended to act.

The ability to control the extent to which liposomes in the blood retain their entrapped drugs is obviously important to those interested in applying them systemically. Although in many cases drugs must be transported intact to where they are needed, in others their gradual release in the circulation may be preferable, especially when membrane barriers will prevent liposomes from reaching target sites.

In the blood, drugs are released from liposomes much more rapidly than expected from normal solute diffusion. Gregory Gregoriadis is at the MRC's Clinical Research Centre, Harrow, Middlesex.

through the bilayers (see reviews). This is attributed to the massive transfer of the liposomal component lecithin to the plasma high density lipoproteins (HDL) in turn leading to the loss of the carrier's integrity and ability to retain solutes (Krupp *et al. Biochem. biophys. Res. Commun.* **72**, 1251; 1976; Scherphof *et al. Biochim. biophys. Acta* **542**, 296; 1978; Chobanian *et al. Biochemistry* **18**, 180; 1979). It now seems that the plasma-induced structural damage to liposomes can be exploited to 'instruct' them either to retain entrapped drugs or release them at predetermined rates. Unilamellar or multilamellar liposomes can be made more stable in the circulation by incorporating cholesterol. Through modulation of phospholipid loss to plasma HDL (Kirby *et al., FEBS Lett.* **111**, 324; 1980), cholesterol controls bilayer permeability to solutes in the blood of injected animals in inverse proportion to its concentration (Gregoriadis & Davis *Biochem. biophys. Res. Commun.* **89**, 1287; 1979; Kirby *et al. Biochem. J.* **185**, 591; 1980). Sphingomyelin also has a similar effect *in vitro* (Finkelstein & Weissmann *Biochim. biophys. Acta* **587**, 202; 1979) although not necessarily by the same mechanism. Liposomes designed to retain their full drug load are expected to minimise the systemic toxicity of such drugs as the antimonials and metal chelators being tested in the intravenous treatment of experimental visceral leishmaniasis (Black *et al. Trans. Roy. Soc. Trop. Med. Hyg.* **71**, 550; 1977; New *et al. Nature* **272**, 55; 1978; Alving *et al. Proc. natn. Acad. Sci. U.S.A.* **75**, 2959; 1978) and iron loading (Guilmette *et al. Life Sci.* **22**, 313; 1978; Young *et al. Br. J. Haematol.* **41**, 357; 1979) respectively.

On the other hand, controlled release of drugs should promote their access to cells (tumours, for example) with which liposomes may not be able to interact directly (Rustum *et al. Cancer Res.* **39**, 1390; 1979). However, toxicity to normal tissues equally accessible to slowly diffusing drugs cannot be excluded. Therefore, for tissues which are amenable to hyperthermia, an alternative approach based on the property of liposomes to become leaky at the melting temperature of their phospholipid component (Yatvin *et al. Science* **202**, 1290; 1978; Scherphof *et al. Biochim. biophys. Acta* **556**, 196; 1979) may prove more useful. In this way, liposomal drugs delivered systemically can be released near and concentrate selectively in, appropriately preheated target areas such as tumours, infected or inflamed tissues (Weinstein *et al. Science* **204**, 188; 1979).

Whether systemic drug release or transport intact to target cells is required, the need for liposomes to persist in the blood for some time seems to rule out the use of the rapidly removed large liposomes (which may nonetheless be preferable for drug transport to the fixed macrophages or

for capture in lung capillaries) and to favour the small unilamellar version. This, when uniformly sized, exhibits a linear rate of clearance and a half life which can be reduced as appropriate by the incorporation of negative charge.

Liposomes may also be introduced into the body other than through the circulation, and here the characteristics of the route of entry also influence the fate and efficiency of action of the liposomal drugs.

For instance, in arthritic rabbits injected intra-articularly with cortisol palmitate anchored on the lipid framework of liposomes, the degree and duration of the anti-inflammatory activity of the steroid is greatest in the initial acute phase of inflammation and is probably related to the phagocytic activity of the synovium (at later phases there are marked changes in its content of cell types) (Shaw *et al. Br. J. exp. Path.* **60**, 142; 1979). Interestingly, a similar beneficial effect of the liposomal steroid has been demonstrated in a few patients with rheumatoid arthritis (de Silva *et al. Lancet* **i**, 1320; 1979).

In another topical use potentially applicable to the chemotherapy of pulmonary metastases, an anti-tumour agent entrapped in positively charged liposomes and administered through the intratracheal route acted in the lung without adverse side effects in other tissues (McCullough & Juliano *J. natn. Cancer Inst.* **63**, 727; 1979).

After injection into tissue (which is of a wider therapeutic scope), liposomes can either disintegrate locally or migrate into the lymph nodes draining the injected tissue (Segal *et al. Clin. Sci. molec. Med.* **49**, 99; 1975). It has now been shown (Osborne *et al. Int. J. Nucl. Med. Biol.* **6**, 75; 1979) that localisation in the primary and secondary regional lymph nodes is enhanced dramatically when small uncharged liposomes are used. In addition to its obvious usefulness in the detection and treatment of tumours of the lymphatic system lymph node localisation of liposomes may also be the cause of their immunopotentiating property (Allison & Gregoriadis *Nature* **252**, 252; 1974; Morein *et al. Nature* **276**, 715; 1978; van Rooijen & van Nieuwmegen *Immun. Commun.* **8**, 381; 1979). This immunopotentiating effect has already shown promise in vaccine development (for example in conjunction with hepatitis B virus surface antigen for a vaccine against hepatitis, Manesis *et al. FEBS Lett.* **102**, 107; 1979).

It has become apparent that ways of controlling the fate of locally applied liposomes can extend beyond simple manipulation of their size and charge. A related development is the finding (Mauk *et al. Science* **207**, 309; 1980) that the rate of disintegration of liposomes in injected tissues can be varied widely by the incorporation of various sugars and amino sugar derivatives of cholesterol into the lipid structure. These derivatives seem to

mediate binding of the associated carrier to the intercellular or cell surface components which, in turn, controls its endocytosis. Such modifications could prove useful in cases where interaction of liposomes with and uptake by cells (for example, gut cells after oral administration) is at present poor or non-existent. □

Io: the electrified satellite

from Garry E. Hunt

OF the 14 Jovian satellites, Io, one of the four planet-sized Galilean moons, presents the greatest anomaly, not only of the Galilean satellites but also among all the other bodies in the Solar System. During the recent Voyager encounters spectacular eruptions were seen on Io which have been initially interpreted as evidence for extensive volcanic activity (Smith *et al. Science* **204**, 951; 1979; Smith *et al. Science* **206**, 927; 1979). But is this the only possible interpretation? Gold (*Science* **206**, 1071; 1979) suggests an alternative explanation of these dramatic observations. He suggests that the passage of Io through the powerful magnetic field of Jupiter induces electric currents in Io's crust which heat up areas of the surface and cause the ejection of volcanic-like plumes of gaseous and solid material. Is this hypothesis possible?

There is no doubt that the eruptions on Io were probably the least expected, and most exciting, results of the Voyager mission. Certainly before the mission, the generally accepted view was that the surface of Io would be heavily cratered rather like the Moon. However Peale *et al. (Science* **203**, 892; 1979) had pointed out that since Io is subjected to resonant gravitational forces exerted by its sister moon Europa, its orbit would be distorted from its approximately circular path. Consequently, Io would be affected also by Jupiter's powerful gravitational field so that this repeated tidal flexing would create an enormous amount of frictional heat in the satellite's interior. This heat would ultimately have to be dissipated through the surface of Io. Would this necessarily result in widespread volcanism?

Smith *et al. (op. cit.)* observed eight active plumes on the first Voyager encounter, of which six were still active at the time of the second flyby three months later. In both cases, material was seen to reach altitudes of 70–280 km at ballistic speeds of up to 1 km s⁻¹ (Cook *et al. Nature* **280**, 743; 1979). Interestingly, all except one of these plumes lie within ±30° of the equator (Strom *et al. Nature* **280**, 733; 1979). The eruption sites appear as regions with a central dark or black irregular to

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circular spot that generally appears to have radiating dark, jet-like streaks. In many ways, the vents mapped from the Voyager imaging data appear to resemble closely terrestrial calderas or pit craters (Masursky *et al.* *Nature* 280, 725; 1979). The floors of these features range from externally shallow to about 4 km in depth. However at least 300 caldera-like features have been detected randomly distributed over Io's surface and not therefore controlled by strongly patterned convection cells.

The south polar region is certainly important in these discussions. McCauley *et al.* (*Nature* 280, 736; 1979) have observed white or bluish patches along scarps and faults, particularly in this region. Such features are diffuse, sometimes variable and obscuring the surface, suggesting that they may be cloud produced by gas leaking out of the interior of the satellite and condensing into some form of snow. Certainly, Pearl *et al.* (*Nature* 280, 755; 1979) have detected a tenuous atmosphere of sulphur dioxide, while several observers (Fanale *et al.* *Nature* 280, 761; 1979; Nash & Nelson *Nature* 280, 763; 1979; and Smythe *et al.* *Nature* 280, 766; 1979) indicate the presence of this material on the surface of Io. The surface is then probably a mixture of sulphur and sulphur dioxide. So there may be reservoirs of liquid sulphur dioxide on Io analogous to the lakes and oceans of the Earth. How therefore can we account for the plume features?

In certain locations, the observations suggest that ice clouds are issuing from fractures in Io's crust, and there is no doubt that liquid sulphur dioxide would escape to the surface along a fault or at the base of a scarp. Certainly, as it reaches the surface the sudden reduction in pressure to below the critical point would cause the liquid to explode into an ice fog that would spread out and then ultimately fall back to the surface again. The process may also erode material along the scarps as well, as McCauley *et al.* (*op. cit.*) suggest. Could this procedure account for the larger plumes that have been observed?

Smith *et al.* (*op. cit.*) suggest that this is the case, with the liquid sulphur dioxide causing violent reactions. This model requires large segregated pools of sulphur below the satellite's surface, and there are certainly some volcanic-like flows that may be of pure sulphur as Sagan (*Nature* 280, 750; 1979) suggests.

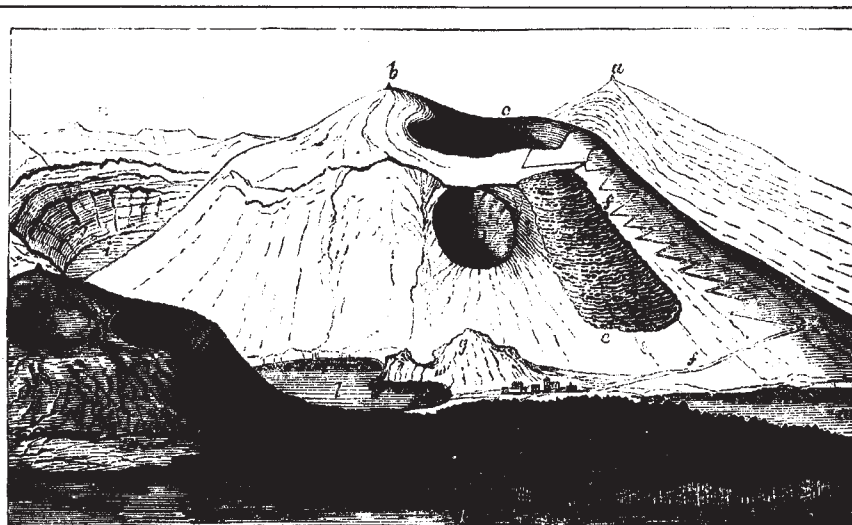
However, an alternative view is taken by Carr *et al.* (*Nature* 280, 729; 1979) who suggest that the volcanism is not primarily driven by the tidal forces, but by a mechanism in which the sulphur-enriched silicate magma erupts through a silicate crust enriched in sulphur. The variations in the physics and chemistry of the magma chambers may then account for the different types of eruption and therefore the different features on Io. Certainly it is difficult to imagine that volcanism on Io has continued at the same rate throughout the history which is implied by the tidal

heating model. The other volcanic bodies, Mars, Venus, Moon and Earth, have certainly had variable periods of volcanism. So why should Io be different?

Gold (*op. cit.*) however, suggests that all these geologically-based interpretations are unsatisfactory. While there is no disputing the altitude and speed of the material in these plumes, he suggests that such behaviour is unlikely for sulphur compounds under volcanic conditions. He indicates that for such material to reach the observed speed of up to 1 km s^{-1} , it would have to be heated to about 6,000 K. Certainly the temperatures that can be expected in any volcanic region are likely to be below 1,500 K for nearly all rock-forming minerals. Furthermore, volcanic activity is supposedly more extensive on Io than on the Earth, so that the internal heating of Io would therefore be greater. But Gold calculates an Ionian heat flow of only $46 \text{ erg cm}^{-2} \text{ s}^{-1}$ from the data of Peale *et al.* (*op. cit.*) compared with $65 \text{ erg cm}^{-2} \text{ s}^{-1}$ for the Earth.

With these inconsistencies, further examination of the Io eruptions is required. Gold points out that the satellite

resides in the intense Jovian magnetosphere so that it will be electrically heated. Certainly Io, with a density of 3.5 g cm^{-3} , is composed of materials that conduct electricity and currents will flow through it as the satellite moves through the Jovian magnetic field. If this electric arc interpretation is correct, then the outbursts would repeat in a systematic way, controlled by the repetition cycle of the external field configuration. Local hot spots would be created, which is consistent with the observations by Hanel *et al.* (*Science* 204, 972; 1979). The strong concentration of the majority of the plumes around the equatorial region indicates that this mechanism is appropriate in that region. However, in other locations, such as those of the poles, sulphur dioxide venting may be more appropriate. The eruption characteristics of Io may therefore be a complex mixture of volcanism and the results of the special electrical environment in which the satellite resides. Whatever the explanation there is little doubt that Io is in a hyperactive state, with the youngest surface currently known in the Solar System. □



100 years ago

Lipari is about ten and a half square miles in area. The highest point is 1,978 feet above the sea. Everywhere the island betrays its volcanic origin. Tuff, pumice, liparite (quartz-trachyte), and obsidian, are constantly met with; at San Calogero a hot spring (198°F .) pours forth water charged with carbonic acid and sulphuretted hydrogen, while the Bagno Secco discharges steam, sulphurous acid, and (it is said, but I think the statement requires confirmation) hydrochloric acid.

Vulcano is undoubtedly the most interesting member of the group from a volcanic point of view. It lies between four and five miles to the south of Lipari, and contains a semi-active crater, which, as regards its usual dynamic activity, occupies a mean position between Vesuvius in its present state of action, and an actual solfatara like that of Puzzuoli. Sulphur, alum, and boracic acid are the substances procured from the crater. We noticed also sublimates of sulphide of arsenic, and salts

of copper were found in association with some of the aluminous incrustation; also chloride of ammonium. I have been assured by two eye-witnesses that blue and green flames sometimes issue from clefts in the bottom of the crater.

Prof. A. Cossa (*Gazzetta Chimica Italiana*, 1878, p. 235-246) has pointed out that Vulcano furnishes the richest supply known of caesium and rubidium. The Faraglioni, also called *rocca dell' alume*, is a trachytic mass much decomposed by sulphurous and sulphuric acids; potassium-alum is found in its cavities, associated with the sulphates of aluminium and calcium, with chloride of ammonium, and with the alums of thallium, caesium, and rubidium. The most complex mixture of volcanic products hitherto found was discovered by Cossa on the edges of a small fumerole at the bottom of the crater of Vulcano. It was found to consist of the sulphides of arsenic and selenium, chloride of ammonium, boracic acid, sulphate of lithium, together with caesium- and thallium-alums, and traces of the alums of potassium and rubidium. From *Nature* 21, 26 Feb., 401; 1880.

REVIEW ARTICLE

Nuclear weapons and power-reactor plutonium

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With modest design sophistication, high-burn-up plutonium from power reactors can produce powerful and predictable nuclear explosions. There is no way to 'denature' plutonium. Power reactors are not implausible but rather attractive as military production reactors. Current promotion of quasi-civilian nuclear facilities rests, dangerously, on contrary assumptions.

NUCLEAR policy, especially in Europe, has often been justified by the belief¹⁻¹⁰ that for making nuclear bombs, 'reactor-grade' plutonium produced by the normal operation of uranium-fuelled power reactors is necessarily much inferior to specially made 'weapons-grade' Pu: so inferior in explosive power or predictability that its potential use by amateurs is not a serious problem and that governments would instead make the higher-performance weapons-grade Pu in special production reactors.

Although that belief is false it was vigorously asserted during 1978-79 by responsible Ministers or by Prime Ministers in at least three high-technology nations. This was apparently because some of their nuclear experts did not know differently, and rejected contrary official US statements as being exaggerated or even politically motivated; or because those experts who did know were not asked; or because correct technical advice was lost, oversimplified, or garbled in transmission through advisors who did not understand the physics. Here I attempt to clarify the properties and performance of various grades of Pu, outlining the physical logic explicitly enough to ensure understanding although discreetly so as not to help the malicious: certain details and technical references have, therefore, been omitted and some calculations treated in conclusory fashion.

The possible military utility of power-reactor Pu has caused widespread professional confusion since 1946. Although some leading scientists appreciated even then^{1,11} that it was useable in bombs or might become so, the contrary assumption (admittedly hedged) was made in the Acheson-Lilienthal report^{12,13}. This recommended that certain nuclear activities could be classified as 'safe' because the Pu they produced could not be converted without timely warning into weapons-useable form, and that these activities could thus be carried out by nations if under strict and enforceable international controls. With the radical 1953 Atoms for Peace initiative, the report's finding that international inspections and treaties could not stop proliferation was forgotten, and US nuclear knowledge and materials were distributed worldwide with increasing enthusiasm and decreasing care¹⁴—apparently on the assumption that power-reactor Pu was, or could be made, unsuitable for use in bombs ('denatured'), despite the US Atomic Energy Commission's refutation of this notion¹⁵ in 1952. With this in many signatories' minds, the Non-Proliferation Treaty (NPT) was negotiated in 1967: an important fact to recall when construing the NPT today, even though its text and the International Atomic Energy Agency (IAEA) do not distinguish in quality between Pu made in power or in military production reactors.

Beginning publicly in the early 1970s in the US (earlier in the Soviet Union and France¹⁶), the assumption that power-reactor Pu was unsuitable for bombs was questioned with increasing force^{17,18}. By 1974, authoritative reports^{19,20} had concluded that

reactor-grade Pu could be used even by amateurs to make effective fission bombs, albeit of somewhat reduced and uncertain yield²¹⁻²⁵. Further analyses during 1976-77, mainly at the US weapons laboratories, revealed a still wider spectrum of technical possibilities, and in 1977 the US announced that it had successfully tested a bomb made from reactor-grade Pu^{26,27}. Yet the earlier finding that this material, though useable, was inferior if used in relatively crude bomb designs was widely and wrongly supposed to apply to all designs. In particular, reactor-grade Pu was alleged to be inherently:

- far more hazardous than weapons-grade Pu to people dealing with it; or
- far more likely to cause unintentional explosions; or
- incapable of exploding violently enough to do much damage, or, at worst, to accomplish most military aims; or
- too unpredictable in explosive yield to be acceptable to its users.

Each of these assumptions contains, in certain circumstances, some truth; but each is generally, or can be by plausible counter-measures be rendered, false. Their implication that reactor-grade Pu is not very dangerous, or unlikely to be attractive to governments, is wishful thinking, and causes the proliferation risks of 'civil' nuclear activities to be gravely underestimated.

In recent years, advocates of commercial Pu use, in referring to the bomb-making that might also result, have had to retreat "from the original concept of denaturing to the notion of making do with less than optimal material"¹¹; yet the earlier myth lingeringly distorts policy²⁸. To decide responsibly about nuclear power and nuclear fuel reprocessing, we must know exactly what "less than optimal" means, and hence must cautiously review published physical principles. The only thing more dangerous than discussing this subject is not discussing it; the lesson of Atoms for Peace may yet be that with Pu, we must get our assessments right the first time.

Plutonium production

All nuclear reactors fuelled with uranium²⁹ (notably the 0.7%-naturally-abundant species ²³⁵U) produce ²³⁹Pu by neutron absorption in fertile ²³⁸U. Some of the ²³⁹Pu formed is fissioned; an increasing fraction absorbs successively more neutrons to form higher Pu isotopes, chiefly ²⁴⁰⁻²⁴²Pu, and transplutonic elements³⁰; and some of the resulting ²³⁹⁻²⁴²Pu (plus traces of ²³⁸Pu and related species) survives until the fuel is discharged. Depending^{19,24,25} on the type and detailed design of reactor, the composition of initial fuel, and the manner of operation, especially the burn-up (extent of exposure of the fuel to neutrons), the net Pu production of a 1-GWe power reactor is typically several hundred kg yr⁻¹, for example ~210-240 kg yr⁻¹ for a light-water reactor (LWR), the dominant commercial type.

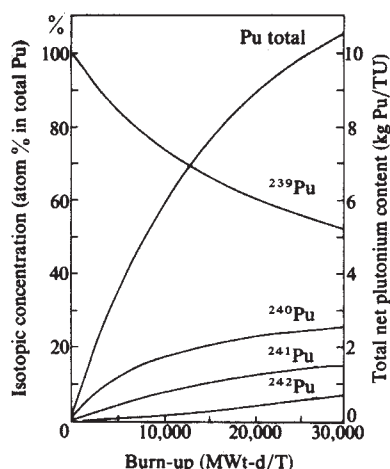


Fig. 1 Typical total amount and isotopic composition of plutonium in discharged fuel as a function of burn-up in a light-water reactor³². The exact values depend in detail on reactor design and operation and on initial fuel composition. Higher isotopes of plutonium and transplutoniums become more abundant in repeatedly recycled fuel.

For a given reactor, the isotopic composition of the discharged Pu depends predictably on burn-up. If each metric ton of uranium (TU) yields only a few gigawatt-days' thermal energy (GWt-dT), neutron capture is so limited that nearly pure ²³⁹Pu—'weapons-grade' Pu—is produced. It contains no more¹ than 7%²⁴ or 8%¹¹ ²⁴⁰Pu, typically³¹ around 6%; perhaps 0.5% ²⁴¹Pu; negligible ²⁴²Pu and ²³⁸Pu.

Higher burn-up, whether through leaving the fuel in the reactor longer or exposing it to a more intense neutron flux, produces a larger proportion of the higher Pu isotopes (Fig. 1). Low-enriched uranium fuel (the usual kind) left for the full 3–4 yr in a reliably operating LWR is usually designed for a nominal burn-up of 27–33 GWt-dT. The latter corresponds³³ to discharge Pu containing ~58% ²³⁹Pu and 11% ²⁴¹Pu (both fissile) plus 25% ²⁴⁰Pu, 4% ²⁴²Pu, and 2% ²³⁸Pu. This composition is broadly similar for other thermal or fast reactor types, except for graphite-moderated reactors³⁴ (²⁴⁰+²⁴²Pu ~ 20%) and fast breeder radial blankets³⁰ (~ 4%). In some circumstances the ²⁴⁰+²⁴²Pu fraction can rise from a nominal ~29% to as much as 49% (34% ²⁴⁰Pu, 15% ²⁴²Pu)³³ in equilibrium LWR Pu recycle fuel; this is unusually high and approximates a practical limit.

Power reactors also can, and often do, discharge fuel short of its full design burn-up. Mature US LWR cores routinely attain well below design burn-up³⁵. Real or simulated malfunctions, such as leaky fuel cladding, may lead the operator to discharge fuel at very low burn-up¹. Alternatively, manipulation of fuel rods can produce a core with high average burn-up but containing some rods of much lower burn-up. 'On-load-refuelling' reactors such as Magnox and CANDU are suitable for clandestine introduction, brief exposure, and removal of small but adequate amounts of fertile material in a few fuel channels. Such methods are not necessarily easy to detect even if an inspector were continuously present, and would probably not be detected at all by present international safeguards³⁶.

Because burn-up, and hence isotopic composition of discharge Pu, can vary enormously between and within reactors and with time, 'reactor-grade Pu' is not a well-defined term. Weapons-grade Pu, which is fairly well-defined (supra), can be readily produced in any power reactor without necessarily and significantly decreasing efficiency, increasing costs, or being detected. But though that option is always open, we assume here that it is not—that power reactors will be used to produce only high-burn-up Pu. We also assume that 'reactor-grade Pu' implies a ²⁴⁰+²⁴²Pu content of ~30%; higher, even arbitrarily higher, even-isotope content will not affect the argument, while a lower content would strengthen it. On these conservative assumptions, the Pu discharged from power reactors will be shown to have major military potential.

Plutonium properties

Relevant nuclear properties of the common Pu isotopes are summarised in Table 1. The values given for m_c are not the quantities needed to make a bomb, as neutron reflection and implosion can reduce critical mass by a large factor. This factor has been officially stated to be ~5, consistent with the US³⁹ and IAEA requirement of strict physical security measures for quantities of Pu ≥ 2 kg (independent of isotopic composition). Published data suggest, however, that with sophisticated design the factor may be >5. For example, in its densest (α -phase) allotropic form, ²³⁹Pu at normal density in a thick Be reflector has a reported critical mass as small as $m_c/4$, and large reflector savings are also obtainable with nonmoderating (and partly fast-fissionable) reflectors such as ²³⁸U. Further, if the core and reflector are equally compressible and if the ratio of reflector thickness to core radius remains constant during compression, critical mass varies as the inverse square of core density. Densities 'several times' normal are said to be attained in military

Table 1 Some properties of plutonium^{31,34,37,38}

Isotope	Decay properties			Heat (W kg ⁻¹)	m_c^* (kg)	Fast-fission		Spontaneous fission	
	Half life (yr)	Main emission (MeV)	Specific activity (Ci g ⁻¹)			$\bar{\nu}^\dagger$	$\sigma_f^\ddagger$ (barn)	Rate (n g ⁻¹ s ⁻¹)	$\bar{\nu}_{SF}^\S$
²³⁸ Pu	86.4	5.5 α	17.4	567	9	~3	2.5	2,600	2.3
²³⁹ Pu	24,390	5.2 α	0.061	1.9	10	3.1	1.9	0.03	2.9
²⁴⁰ Pu	6,600	5.2 α	0.23	7.0	40	3.4	1.3	1,020	2.2
²⁴¹ Pu	13.2	0.021 β	112	4.5	12	3.2	1.8	—	—
²⁴² Pu	387,000	4.9 α	0.0038	0.1	90 [¶]	3.3	1.2	1,670	2.3
²⁴¹ Am #	433	5.5 α	3.43	106	114**	—	—	0.623	3.1

* Approximate bare-sphere prompt-critical mass at normal density; Pu is α -phase ($\rho = 19.8$ g cm⁻³). For comparison, m_c for 93.5% ²³⁵U ($\rho = 18.8$ g cm⁻³) is 49 kg ²³⁵U.

† Approximate gross neutron yield per fast fission (Argonne 16-group).

‡ Approximate fast-fission cross-section (Argonne 16-group). (The capture-to-fission ratios are also important, and tend to be high for even Pu isotopes.)

§ Approximate neutron yield per spontaneous fission.

|| Values cited by De Volpi³⁷, who gives the ²³⁸Pu m_c as 7 kg (unpublished); the best value calculated for α -phase, however, is the $m_c \sim 9.2$ kg shown here (R. W. Selden, personal communication).

¶ Best Livermore estimate from the range 75–100 kg (R. W. Selden, personal communication). De Volpi³⁷ assumes ~95 kg (or 118 kg in Appendix H), but used ≥ 156 kg in earlier publications^{45,46}. Calculated m_c is probably not finite for ²⁴²Pu ¹⁰B₂, owing to threshold effects, but is ~350 kg for ²⁴⁰Pu ¹⁰B₂ at $\rho = 11.5$ g cm⁻³ (R. W. Selden, personal communication).

Daughter of ²⁴¹Pu, important (like the trace isotope ²³⁶Pu) mainly for its γ emissions.

** Approximate estimate by Clayton³⁸ for $\rho = 11.7$ g cm⁻³, implying reactivity comparable with ²⁴⁰Pu.

bombs⁴⁰, and by means described in the open literature a slightly subcritical mass of α -phase ^{239}Pu in a U reflector can be compressed to 1.85 times its initial density, corresponding to a reactivity increase of ~ 3.4 times. The same method can yield even higher compressions. Although high compression is inconsistent with simultaneous high reflection, it may be possible to achieve significant supercriticality with initial ^{239}Pu masses under 2 kg. Regardless of the exact figure, the IAEA's 8-kg 'significant quantity' design basis for detecting diversions³⁶ seems far too high.

Of the Pu isotopes in Table 1, only ^{239}Pu and ^{241}Pu are fissile, that is, fissionable by thermal (slow) neutrons. All Pu isotopes, however, are fissionable by the fast neutrons in a bomb: indeed, at energies > 1 MeV (69% of fission neutrons) the fission cross-section of ^{240}Pu is less than that of ^{239}Pu by a margin of less than 20%, so the amount of ^{239}Pu required to form a normal-density critical mass is remarkably insensitive to $^{240+242}\text{Pu}$ content (Table 2). Published neutron transport calculations confirm that the even isotopes produce only minor changes in reactivity, neutron spectrum, and mean prompt-neutron lifetime. So reactive is ^{240}Pu that changing the $^{240+242}\text{Pu}$ content from 6 to 30% increases m_c only from ~ 11 to ~ 13 kg³¹. No known fast-neutron absorber can make Pu of any practical composition incapable of forming a prompt-critical mass^{31,42}: calculations⁴² suggest that substituting the best fast-neutron absorber known, ^{10}B , for oxygen in reactor-grade crystal-density PuO_2 ($m_c \sim 35$ kg) would increase m_c only to ~ 70 kg.

Fast-fission properties of Pu, then, are only slightly affected by ordinary changes in isotopic composition. The neutron background is, however, modestly affected. Spontaneous-fission neutrons (Table 1) provide typically³⁴ of the order of $100 \text{ n g}^{-1} \text{ s}^{-1}$ in weapons-grade Pu, about 500 in reactor-grade Pu. A further contribution (at lower neutron energies) comes from (α, n) reactions with light-element impurities. In Pu metal this is not an important neutron source³⁴, but it can more than double the neutron background in PuO_2 , as 1 Ci of α -emitter bombarding oxygen produces of the order of $5,000 \text{ n s}^{-1}$.

Neutron background from all sources is significant for weapons physics (infra) and makes reactor-grade Pu give somewhat higher radiation doses than weapons-grade Pu. For long-term commercial handling within the normal canons of health physics, shielding would be required. For clandestine weapons manufacture it would not, because the published total dose rates (mainly γ and X rays) are relatively modest—of the order of rem h^{-1} at the surface of a 1-kg fresh recycled PuO_2 sphere, $< 1 \text{ mrem h}^{-1}$ at 1 m. Even under extreme assumptions (18½% ^{238}Pu , 30% $^{240+242}\text{Pu}$, 10-kg PuO_2 sphere with subcritical multiplication included), neutron dose rates (60 mrem h^{-1} at 1 m) "do not provide an effective deterrent"⁴⁴. It is obviously not correct that "slight mistakes in the knowledge of exact [isotopic] composition . . . may well pose extreme radiological hazards"⁴³, given normal precautions against inadvertent criticality.

The specific activity of reactor-grade Pu is typically⁴² $\sim 10 \text{ Ci g}^{-1}$ as against 3 Ci g^{-1} for weapons-grade Pu, the neutron background (for metal) and the inhalation toxicity ~ 5 times higher, and the heat production $\sim 10 \text{ W kg}^{-1}$ (about the same as for 1-yr-old spent LWR fuel) as against 3 W kg^{-1} . Only a difference of orders of magnitude in these quantities—the extent by which they all exceed the corresponding values for ^{235}U —would reflect differences in ease of handling that would be important in designing new bomb-making facilities⁴².

Thermal denaturing^{44–46} of reactor-grade Pu was recently proposed by A. K. Williams *et al.* (unpublished Allied-General Nuclear Services) and A. De Volpi³⁷. The ^{238}Pu content would be increased from its normal 1–2% (nearly 5% in some recycle Pu^{33}) to 10–15%, perhaps nearly 20%, chiefly by recycling ^{237}Np (itself a bomb material with $m_c \sim 75$ – 105 kg) with ^{232}Th rather than ^{238}U diluent²⁹. The ^{238}Pu would increase heat production to 6–9 times normal. Some calculations⁴⁴ based on cores of high mass and high volume-to-surface ratio, in direct contact with non-thermally-stable explosives, suggest serious

Table 2 Critical mass of plutonium spheres in a ~ 10 -cm natural uranium reflector as a function of plutonium isotopic composition^{41*}.

$^{240+242}\text{Pu}$ (atom %)	^{239}Pu in critical mass (kg)	Total Pu in critical mass (kg)
0	4.4	4.4
10	4.5	5.0
20	4.5	5.6
30	4.6	6.7
40	4.7	7.8
50	4.8	9.6

* Assuming $^{240}\text{Pu}/^{242}\text{Pu}$ ratio similar to that shown in Fig. 1.

design problems. But realistic choices of geometry and materials can readily overcome these problems. Cooling does not even become an interesting design problem until the ^{238}Pu content approaches that of a thermoelectric heat source, and a much lower content, well over 20%, does not provide an effective deterrent even to most amateurs, though it would make safe and economic fuel-cycle operations hard to envisage⁴⁷. Only in quite incompetent hands could the extra heat pose a danger of unplanned detonation.

A second 'denaturing' proposal by De Volpi³⁷ would combine ^{238}Pu and ^{240}Pu with extra ^{242}Pu , which is a diluent in fast spectra and something of a neutron poison in thermal spectra⁴⁸. Pathologically high ^{242}Pu content would increase m_c , though not by the ~ 30 times claimed by Olds⁴⁵ (compare Table 1); as all Pu isotopes have "reasonably small critical masses, this concept [of denaturing by dilution] is not applicable to plutonium"⁴⁴. De Volpi states⁴⁶ that fuels made mostly of ^{242}Pu and with a fissile fraction as low as 18% are useable even in present fast reactors, but he does not analyse performance or economics, which apparently offer serious difficulties⁴⁸, and his analysis of weapons physics seems deeply flawed.

Synergisms are negligible, so the effect of each even Pu isotope can be dealt with separately: thermal 'denaturing' with ^{238}Pu above and neutronic 'denaturing' with all three isotopes below. Practicable dilution with ^{242}Pu cannot alter design constraints enough to affect the conclusions below.

Finally, nonmetallic forms of Pu must be considered. Reactor-grade Pu can be used directly in bombs without reduction to metal (though metal generally gives better performance). The oxygen in PuO_2 dilutes the Pu and lengthens the 'generation time' between fissions, reducing the yield, but it also slightly compensates by moderating the neutrons to lower energies where the fission cross-sections are higher. The dilution effect predominates and roughly doubles⁴² the δ -phase metallic m_c . It also alters other design parameters. Nonetheless, the oxygen is not a neutron poison and does not prevent attainment of "large reactivity coefficients and short neutron life times"¹⁸ even in the much less reactive $^{235}\text{UO}_2$. Indeed, the low initial density ($\rho \sim 2.3 \text{ g cm}^{-3}$ uncompact, 4 – 5 g cm^{-3} moderately compacted) of PuO_2 powder relative to its sintered (≈ 11.2) or crystal (11.5) density, and its relative compressibility at crystal density, permit crude designs with a generous safety margin of initial subcriticality to achieve high supercriticality after implosion. It is, therefore, not surprising that PuO_2 has been uniformly agreed to be directly useable in formidable explosives^{18,19,24,25,41}. A bomb made directly even from fresh LMFBR mixed-oxide fuel (15–25% Pu) is theoretically possible⁴⁹, though unwieldy.

Weapons physics and reactor-grade plutonium

A nuclear explosion results from a divergent chain reaction in a prompt-supercritical mass: that is, one which can support a chain reaction by virtue only of the prompt neutrons released immediately by fission. The fission neutrons in a bomb are fast, with energies in the megavolt range and velocities of the order of 1 – $2 \times 10^9 \text{ cm s}^{-1}$. The fissionable material must be of sufficient

size and density that a neutron born within it is likely to cause a further fission within it. The critical masses discussed above imply that the mean distance between fissions is of the order of centimetres, hence that the mean time between fissions is of the order of 10^{-8} s. Roughly "40–50 generations of fissions are required to build up a fast chain reaction to an explosive level"⁴¹: $e^{40} = 2.4 \times 10^{17}$ fissions would release 1.6×10^3 kcal, equal to the nominal energy release from ~ 1.6 kg of high explosive and thus approaching the energy density needed to disassemble rapidly a Pu core of nominal size. Only the last few generations in this exponential process provide appreciable energy yield. That energy builds up, in a few hundredths of a microsecond, temperatures of several hundred million °C and pressures of the order of 10^8 bar, causing the core to expand with a velocity of the order of 10^8 cm s⁻¹. Expansion from the initial radius by a factor roughly equal to the sixth root of the number of critical masses present, that is, by ~ 1 cm, makes the mass subcritical and quenches the chain reaction. Once the explosion begins, then, only a few more generations of fission, producing most of the yield, are possible.

The designer seeks to assemble as supercritical a mass as possible (by 'inserting reactivity') as quickly as possible, and to inject neutrons to initiate the chain reaction at the optimal moment during that assembly—before the instant of maximum supercriticality, so that the bomb's tendency to fly apart is partly countered by the continuing forces of convergent assembly. The yield of the nuclear explosion depends strongly on the degree of supercriticality achieved when the chain reaction is initiated. If the neutron background is so large that preinitiation, before the optimal moment, is likely, then the yield varies¹⁸ as (rate of reactivity insertion)^{-1-1.5}.

Preinitiation reduces yield according to the Poisson statistics of neutron background, and can be counteracted by faster assembly. For a constant level of maximum reactivity insertion, the probability of avoiding preinitiation varies as $1/\exp$ (neutron source strength $\times$ assembly time).

Preinitiation is a problem faced by any nuclear weapons designer using any fissionable material³¹. With ²³⁵U (spontaneous fission rate 8×10^{-4} n g⁻¹ s⁻¹), it is a mild problem, so assembly by the relatively slow 'gun' method at published rates < 1 mm μ s⁻¹ (0.3 mm μ s⁻¹ in the Hiroshima bomb) suffices. But even weapons-grade Pu, with neutron background $\geq 60,000$ times higher (just above ²³⁸U), preinitiates unless assembled implausibly by a convergent arrangement of chemical high explosives. The radial compression rate can then³² exceed 2 mm μ s⁻¹.

A reflected core of Pu metal, sufficiently subcritical that neutron multiplication can be neglected, will have a neutron background of the order of 0.5×10^6 n s⁻¹ if of weapons grade, several million n s⁻¹ if of reactor grade. The former figure implies a mean time between neutrons of a few microseconds—half an order of magnitude longer than the duration of the fission chain. But the latter figure implies a mean time between neutrons that is short compared with the time required to complete the assembly of a highly supercritical mass, unless that assembly is extremely rapid, implying very high shock velocities and compression. This can in fact be achieved:

"Plutonium of any feasible grade (weapons or reactor) is unsuitable for the gun-assembled systems because the neutron background and relatively long assembly time introduces significant preinitiation probabilities. This is not necessarily true for implosion types"³⁴.

Preinitiation, then,

"... does not necessarily make an explosive unreliable. Preinitiation does result in a statistical uncertainty in the yield ... [that] is statistically distributed between predictable upper and lower limits which are likely to be more than a factor of 10 apart. For a well-understood design properly constructed, however, the most probable yield range could be predicted within much closer limits"²⁴.

"In implosion devices, preinitiation probabilities may be lowered by various design techniques. Even relatively low

technology designs, notwithstanding the variability in yield, can produce effective, highly powerful weapons"³⁴.

This can be achieved⁴¹ even with a neutron source strength of the order of 10^6 n s⁻¹. As was officially appreciated in 1944, "... [A] rough quantitative analysis of the assembly velocities attainable with very large charges of high explosive ... suggested that because of the strong focusing effect of the converging material, one could introduce a strong steady source of neutrons into the bomb (for example, by deliberately leaving the material in an impure state), and still beat the chain reaction and attain complete assembly".

Thus preinitiation "... may mean a statistical uncertainty in the yield within a predictable range. Increasing technological sophistication will reduce this uncertainty"³¹.

Now, consider several levels of "increasing technological sophistication" and their likely effects on the performance of implosion bombs made from reactor-grade Pu or other compositions³⁷ with high neutron source strength.

Performance as a function of design

Since it became public knowledge that construction of illicit nuclear weapons by non-state adversaries must be taken seriously¹⁹, and that reactor-grade Pu is suitable for such bombs^{17,18,24}, the level of technology on which most discussions have centred can be described as 'crude amateur designs' in which the normal military design requirements for pure fissile material and for the symmetry, simultaneity, and speed of implosion are very considerably relaxed. The canonical description of such designs is that of Willrich and Taylor¹⁹:

"Under conceivable circumstances, a few persons, possibly even one person working alone, who possessed ~ 10 kg of plutonium oxide and a substantial amount of chemical high explosive could, within several weeks [or perhaps less], design and build a crude fission bomb. ... [that] would have an excellent chance of exploding, ... probably ... with the power of at least 100 tons of chemical high explosives. This could be done using materials and equipment that could be purchased at a hardware store and from commercial suppliers of scientific equipment for student laboratories. ... [It] might yield as much as 20 kilotons of explosive power—the equal of the Nagasaki A-bomb [though the probability of such a high yield is quite small]."
"... very sophisticated thermal-hydraulic and neutronic calculations"⁴³ would not be needed. Several suitably comprehensive literature searches have in fact been conducted by amateurs. The bomb could fit in a car⁴¹.

Making an effective, transportable fission bomb is not a trivial task. Safely realising a paper design in properly working apparatus would require alertness to subtleties and care and skill in technical arts (which many criminal enterprises have shown). The necessary human resources will be assumed here to have been obtained. The skills required for both design and fabrication naturally increase with increasing sophistication and have been taken into account in the policy conclusions drawn here.

Several studies^{32,43,50,51} have dealt quantitatively with the heterogeneous class of flexible and imprecise designs grouped here as Level One technology. Calculations confirm that in the absence of gross incompetence or malfunction of major components, Level One technology is extremely likely to yield > 0.01 kton, likely to yield in the range 0.1–1 kton, able on occasion to yield several kton, and unlikely to yield 10–20 kton.

A second level of technology might be characterised as 'imitation Trinity designs' or as 1945-vintage US technology. It uses special high-explosive components and detonators (all of which are commercially available) in a straightforward geometry to compress an accurately made metallic Pu core. Given the materials and information that have become widely available since the 1940s, such a technology might be typical of a low-level national effort to produce a bomb that can be depended on to work well without previous testing (Trinity yielded 17 kton). It is

not a clever technology (simpler means can produce better results) but is basic and reliable, and has been the subject of several amateur design exercises. Five distinguished nuclear weapons experts concluded that using weapons-grade Pu (or ^{233}U or highly enriched ^{235}U)

"... it is possible to design low-technology devices that would reliably produce explosive yields up to the equivalent of 10 or 20 kilotonne of TNT. With reactor-grade plutonium it is possible to design low-technology devices with probable yields 3–10 times lower than those mentioned above (depending on the design), but yields in the kiloton range could be accomplished. Militarily useful weapons with *reliable* nuclear yields in the kiloton range can therefore be constructed using low technology and reactor-grade plutonium"²⁴.

(This is consistent with De Volpi's Table L-6 results³⁷, given realistic choices of parameters.) As for the resources required, "a small group of people, none of whom have ever had access to the classified literature", could get by with "modest machine-shop facilities that could be contracted for without arousing suspicion" and with "a fraction" (perhaps a small fraction) of a million dollars for open-market equipment²⁴.

Recently declassified documents dealing with 1945 US technology give¹

"... quite precise quantitative information ... covering some aspects of how the probability distribution of nuclear yields changes with the isotopic composition of the plutonium used. ... This information makes clear that with power reactor grade plutonium, an implosion weapon of even the simple kind first used by the US would reliably have yields between 1 and 20 kton"⁵².

Preinitiation at the least favourable moment⁵⁰ in a Trinity-type bomb would still produce¹ reliable kiloton yields: the worst-case, minimum, 'fizzle' yield is still a "militarily useful"³¹ ~1 kton. This behaviour is chiefly a function of assembly rate, not neutron background, because the least favourable moment cannot get any less favourable. The same conclusion would therefore hold⁴² even with arbitrarily high neutron source strength, as from 'a large fraction' of ^{242}Pu (ref. 46) and high ^{238}Pu (ref. 37). Contrary to Meyer *et al.*⁴³, "slight mistakes in the knowledge of exact isotopic composition" could not "lead to neutralisation of the explosive design" and could indeed be readily accommodated by design.

Selden summarises³¹:

"It is likely that a nuclear explosive designer would choose to minimise the ^{240}Pu concentration, given the choice. However, an entirely credible national nuclear explosives capability could be constructed using only reactor grade plutonium."

Of course, the designer may choose to avoid the extra fiscal and political cost (if detected) of the *unambiguously military* dedicated facilities required¹³ to make large amounts of the more conveniently useable weapons-grade Pu. Some governments may find advantages, notably civilian 'cover', in doing the best they can with their plentiful high-burn-up Pu instead. Recent classified analyses have therefore explored further levels of technological sophistication that can overcome the sub-optimal features of high-burn-up Pu and increase the ~1-kton *minimum* yield of Level Two technology.

Perhaps the most categorical statement of the results comes from a speech¹⁴ by Commissioner Gilinsky (emphasis added):

"... [S]o far as reactor-grade plutonium is concerned, the fact is that it is possible to use this material for nuclear warheads at all levels of technical sophistication. In other words, countries less advanced than the major industrial powers but, nevertheless, possessing nuclear power programs can make very respectable weapons. And, I might add, these are the very countries whose names turn up in every discussion of proliferation. Of course, when reactor grade plutonium is used there may be a penalty in performance that is considerable or insignificant, depending on the weapon design. But whatever we might once have

thought, we now know that even simple [Level Two] designs, albeit with some uncertainties in yield, can serve as effective, highly powerful weapons—reliably in the kiloton range."

The italicised passages imply that further levels of technology exist with still higher yield and predictability than Level Two.

A third level of technology seeks to overcome preinitiation by extremely rapid assembly. The necessary rates of assembly can be calculated and seem to be readily attainable. One published configuration, for example, is stated to be able to compress a sizeable core at several times the $2\text{ mm }\mu\text{s}^{-1}$ radial rate mentioned earlier. Far higher rates are possible with this method, because in a convergent implosive system, shock pressures vary roughly as the inverse fourth power of radius and shock velocities as the inverse square of radius. Applying the same design to a small core can therefore achieve such high assembly velocities that the shock can traverse much of the core and insert very substantial reactivity before hydrodynamic disassembly forces can dominate. The probability of preinitiation then becomes small, the expected yield relatively large, and its dispersion small; in short, the performance penalty approaches the "insignificant"¹⁴.

Calculations suggest that this Level Three technology is sufficient, using reactor-grade Pu, for almost any military objective, even with attempted 'denaturing'³⁷. The method will readily occur to most governments and to many technically informed amateurs. The apparatus is not unduly difficult to achieve. It does not necessarily involve a higher technology than Level Two, and should be considered more a logical extension of Level One, a 'smart amateur design', than the exclusive province of governments. It does not necessarily require nuclear testing to ensure confidence in obtaining high yield, provided the maker is confident that the well-characterised non-nuclear components will function as designed. Non-nuclear test firings would, of course, increase this confidence.

Most military bombs are required to function normally in high neutron fluxes such as might arise from nearby nuclear explosions. Essentially the same design considerations apply as in the case of high internal neutron source strengths. It can be safely presumed that these problems are routinely overcome by various means, including thermonuclear techniques that could render the penalty from using reactor-grade Pu not only very small but nil, even at very high yields. This is a very high technology requiring elaborate theoretical, computational, and fabrication facilities, together with prior nuclear testing. But such sophistication is not required for governments or even for some subnational groups to extract from reactor-grade Pu, using Level Three technology, the kind of yield and predictability that the major nuclear powers would have found satisfactory for inclusion in their arsenals around the early 1960s.

Weapons effects and the implications of uncertain yield

Fissioning 1 kg of Pu yields $(2.5 \times 10^{24} \text{ fissions}) \times (\sim 180 \text{ MeV of prompt energy per fission}) \approx 7.3 \times 10^{13} \text{ J kg}^{-1}$ or $\sim 17 \times 10^{12} \text{ gcal kg}^{-1} \approx 17 \text{ kton kg}^{-1}$. This 17-kton yield (Hiroshima was 13 kton, Nagasaki 22 kton) corresponds to the conversion of a mass defect of only 0.8 g. But unlike chemical high explosives, some of the yield of nuclear explosives appears not as blast or heat but as prompt electromagnetic radiation at many frequencies, especially γ rays, and as prompt neutrons. The smaller the nuclear yield, the more the effects of the nuclear explosion are dominated by prompt radiation.

For example, a 'crude amateur design' yielding only 0.1 kton—which corresponds to fissioning only 6 g (a nominal efficiency of the order of 10^{-3}) and converting a mass defect of 5 mg—typically produces^{19,53} 500 rem of prompt γ dose (roughly the LD_{50} , or dose likely to kill half those exposed to it) at unshielded ranges up to 300 m, plus 500 rem of prompt neutrons ($\sim \text{LD}_{50}$) to ~450 m, plus 500 rem of fallout exposure ($\sim \text{LD}_{50}$) to 300–1,000 m for people lingering for an hour. Yet such a surface burst makes a crater only ~14 m in radius. Blast

damage is also of shorter range than the prompt radiation—severe (overpressure to 10 lb in⁻² = 0.68 bar) to 150 m and moderate (3 lb in⁻² = 0.20 bar) to 300 m. The relatively limited blast damage, even at such low yield, however, could amplify the radiation effects by $\sim 10^3$ times if used to induce a 1% ground release from an operating 1-GWe LWR (16-GCi inventory), ~ 10 –100 times more from a reprocessing plant.

Effects of larger yields are readily, if roughly, calculable from standard scaling laws^{19,53}. For example, a yield of 1 kton, a practical minimum with Level Two technology (but three orders of magnitude larger than a World War II blockbuster), would devastate several km², with 500 rem prompt radiation beyond 700 m and with 500 rem fallout around 1–3 km. If a yield Y expected to be 8 kton is in fact only 1 kton, the blast area will diminish not by 7/8 but by 3/4 (as $Y^{2/3}$), and the lethally irradiated area only by half (as $Y^{1/3}$) (refs 1, 53). Such reductions would generally be smaller than the variability in effect expected from the varying circumstances of use; and except in special tactical-warfare conditions, the important thing is not whether the designer can predict the exact yield, but rather that the potential victim cannot.

Conclusions

The above discussion has sought to provide a discreet, selective, but adequate physical basis for understanding the scope for using reactor-grade Pu in fission bombs at some of the diverse levels of sophistication open to various potential users (the taxonomy given is not exhaustive). 'Denaturing' Pu by adding to it, singly or in combination, essentially inseparable⁵⁴ neutron-emitting diluents such as ²³⁸Pu, ²⁴⁰Pu, ²⁴²Pu, or ²⁵²Cf (ref. 55)—or indeed any other interfering material that cannot be readily removed, for example, by ion exchange—is "fallacious" and "not a valid concept"³¹. (Dilution with UO₂ or other materials requiring chemical or physical⁵⁶ separation is a valid cess^{19,25,34}—but does not solve the problem.) Taking all effects on weapons physics into account, a high ^{238,240,242}Pu content may reduce expected yield to a level that could devastate only a reduce expected yield to a level that could devastate only a modest portion of a city rather than all of it, and may make that yield much less predictable, if the bomb is crudely made. But these faults can be overcome by more clever design, without necessarily using high technology, and at Level Three this can be done by gifted amateurs. It is therefore incorrect to state categorically that bombs made from reactor-grade or deliberately 'denatured'³⁷ Pu are less effective, less powerful, or less reliable than those made from weapons-grade Pu. Whether these reservations hold, and whether by a meaningful margin, depend on the designer's intentions, skills, and resources, all of which may be unknowable. And the implication that the effects of even a crude, minimal 0.1–1 kton explosion would be tolerable for a free society is at best disingenuous^{19–21,27}.

The foregoing argument also implies that power reactors are not an implausible but are rather potentially a peculiarly convenient type of large-scale military Pu production reactor. This goes beyond the proposition that

"... in situations of extreme tension states may turn to second or third best instruments to get their hands on weapons they regard as essential to their security. The point is that, with plutonium readily available, it may be turned to. And those groups within countries that want to go nuclear can pursue an ambiguous path of keeping their options open until the last minute under a commercial disguise"⁵⁷.

A government can either manipulate civil fuel cycles to produce substantial amounts of low-burn-up plutonium, or, especially using Level Three technology, use high-burn-up Pu in bombs with insignificant performance penalty. Regardless of possible technical measures^{24,25,54,58,59}, such Pu will become readily available in quantities of the order of 10^4 – 10^5 m_e yr⁻¹, and in extracted forms useable for weapons within hours or days, if plans proceed for commercial reprocessing, which is unsafe-guardable both today³⁶ and in principle^{14,59,60}. Making even high-burn-up Pu in domestic power reactors incurs no penalty in reactor efficiency or in equipment costs: a reactor-exporting country will gladly build the reactor, train the technicians, and pay for the whole package with generous export subsidies. If extracted, and using any of the numerous means of evading effective safeguards, the Pu discharged from a single large power reactor suffices for about 10² bombs per year, a large weapons programme, and there is the alternative of embezzling up to a few bombs' worth per reactor-year from the fuel cycle within its $\sim 1\%$ statistical 'noise', a form of theft that can be made undetectable in principle. The marginal time and money required to use civil reactors for military production are orders of magnitude less²⁷ than those needed for dedicated military facilities^{11,61}. The extra facilities and staff required could be hidden within the civil programme: the "ideal place to hide a tree is in a forest"⁶¹. And perhaps the greatest attraction of producing military Pu in a power reactor is that it has a civilian 'cover' and thus—at least until regional rivals follow suit—an apparently zero political cost.

In short, the somewhat greater technical difficulty of using power-reactor Pu for effective military bombs—assuming the reactor is actually operated at high fuel burn-up—may be more than counterbalanced by the greater political and economic ease of obtaining that Pu. It "should not be lightly disdained in favour of purer material from dedicated facilities"⁶¹.

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ARTICLES

Permian–Triassic continental reconstruction of the Gulf of Mexico–Caribbean area

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The morphology of the margins of Palaeozoic continental crust around the Gulf of Mexico and Caribbean Sea is derived from the distribution of Jurassic evaporites in the Gulf and the distribution of post-Palaeozoic arcs around the Caribbean. The Permian–Triassic position of the continental masses in this region is determined by fitting these margins together to achieve the best agreement of margin morphology and geological continuity. This model is supported by geological observations from the margins and floors of the Gulf and Caribbean and by geometrical considerations derived from continental reconstructions around the Atlantic.

THE plate tectonic evolution of the Gulf of Mexico and Caribbean Sea is poorly understood because a coherent seafloor spreading history based on magnetic anomalies cannot be determined in these basins. Consequently, evolutionary models in this area must be based largely on ambiguous and less precise geological observations from the margins and interpretation of seismic reflection data from the basins. Due to the geological complexities produced by plate kinematics of even geometrically simple systems¹, this approach may not lead to a definitive model, but it constrains the models possible.

Determination of the Permian–Triassic positions of the continents around the Gulf of Mexico and Caribbean Sea is the most critical aspect of all evolutionary models of this region. I propose here a Permian–Triassic reconstruction of the continents around the Gulf of Mexico and Caribbean Sea that emphasises the geometrical constraints imposed by the pre-Mesozoic margin morphology determined for these continents and the fit of the continents around the Atlantic Ocean. The distribution of Jurassic evaporites has a dominant role in determining pre-Mesozoic margins by delimiting the boundaries of Jurassic basins that formed as a result of continental breakup.

Previous models

Although it has been suggested that the Gulf of Mexico existed during the Palaeozoic^{2–4}, consideration of the stratigraphically controlled seismic reflection data in the Gulf and the geology of the margins of the Gulf and Caribbean support the view that

these basins were formed by continental breakup during the Triassic and early Jurassic^{6–10}. Several reconstructions have been proposed to close the Gulf of Mexico and Caribbean: the solutions are generally of two types (1) closure by juxtaposing North and South America and relocating Mexico and Central America west of their present position relative to North America^{9,11–13} and (2) closure by segmenting and positioning portions of Mexico and Central America between North and South America^{6,7,14}.

The reconstructions of the first group were supported by the recognition of large strike slip faults in Mexico that provided a means to segment and relocate Mexico and Central America during the late Palaeozoic^{4,15,16}. There are also palaeontological, geological and palaeomagnetic data to suggest that South America was very close to North America during the late Palaeozoic^{9,11,17}. However, these data lack the resolution to determine precisely the relative positions of North and South America during the late Palaeozoic, and there are several lines of evidence to suggest that they were not contiguous.

One important argument against juxtaposing South America and North America is the absence of a Palaeozoic magmatic arc on either margin. An arc system culminating in late Carboniferous times should have developed as a result of the convergence that formed the Ouachita Mountains. This problem is usually circumvented by placing an inferred arc beneath the thick Mesozoic and Cenozoic sediments of the Gulf Coast (ref. 11, Fig. 2b, c; ref. 18). However, Wickham *et al.*¹⁹ have shown that this inference is untenable because there are no arc-related, pre-Carboniferous, igneous, metamorphic or sedimentary rocks within the foldbelt; and they interpret the southern margin of North America as a south-facing Atlantic-type margin that

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collided with a southern continental mass containing the magmatic arc in Pennsylvanian times. Northern South America is unlikely to be this mass because there are no late-Palaeozoic plutonic rocks east of the Venezuelan Andes²⁰. The pre-Mesozoic basement to the Coast Ranges of Venezuela seems to be Precambrian rocks of the Guyana Shield that were intruded and deformed during a Cretaceous arc-continent collision²¹.

The paucity of Jurassic evaporites along the northern margin of South America also suggests that closure of the Gulf was not achieved by juxtaposing North and South America as suggested by proponents of the first group. Generally, evaporites formed during initial ocean opening lie on both sides of the resultant ocean^{10,22}. There are no evaporites on the northern margin of South America that are of comparable extent to the Louann and correlative evaporites of the Gulf of Mexico¹⁰, and this strongly suggests that North and South America were not opposing margins to the same developing ocean basin.

The most convincing argument against juxtaposing South and North America during the latest Palaeozoic is that this requires disruption of the early Triassic fit of the continents around the Atlantic. Because continents are torsionally rigid, the reconstructed positions of the peri-Atlantic continents provide the most powerful constraint on the relative position of North and South America²³. Positioning South America against the northern margin of the Gulf of Mexico requires unrealistic offsets of corresponding salt basins and fracture zones along the margins of North America and Africa^{8,22}.

These arguments against the juxtaposition of North and South America support the models of the second group that close the Gulf and Caribbean without this restriction. However, since the models of Carey¹⁴ and Dietz and Holden⁶ were proposed, the Greater Antilles (with the possible exception of part of western Cuba) were found to be of post-Palaeozoic age and therefore they need not be considered in a Triassic reconstruction of this area. Freeland and Dietz⁷ considered this in their model, but, by removing these post-Palaeozoic continental masses, large gaps were left between North and South America. Subsequent examination indicated that Blake-Bahama Platform, which was included in the reconstruction of Freeland and Dietz⁷, is likely to be an early Mesozoic volcanic construction^{8,24} and removal of this platform enhances the problem of large unexplained gaps. In addition, the poor morphological and geological fit of the reconstructed Palaeozoic continental masses as proposed by Freeland and Dietz⁷ is not convincing.

Collectively these arguments suggest that the Atlantic fits proposed by LePichon and Fox⁸ and Sclater *et al.*²⁵ best satisfy constraints imposed by palaeontological, palaeomagnetic, morphological and petrological data. Tighter fits such as those of VanderVoo *et al.*⁹ and Pilger¹³ seem unsatisfactory when the geological evolution of opposing margins of North and South America are considered and the more open fit of Bullard *et al.*²⁶ creates a gap between North and South America that is too large to be filled with the available pre-Mesozoic continent fragments around the Gulf of Mexico and the Caribbean. Additional difficulty in reconstructing this area results from the extensive alteration of the margin morphology of North, Central and South America during the Mesozoic and Cenozoic. Examination of proposed models therefore suggests that a more precise approximation of the Permian-Triassic positions of continents around the Gulf and Caribbean can be obtained by first removing obvious post-Palaeozoic island arcs and sedimentary constructions and then fitting the resultant margins of continental crust back together in the space dictated by the LePichon and Fox⁸ fit of the continents around the Atlantic.

Determination of Palaeozoic margins and proposed reconstruction

The distribution of thick Jurassic evaporites is extremely useful in attempting to define the boundaries of pre-Mesozoic crust that resulted from Triassic rifting in the Gulf of Mexico area. The landward boundaries of these deposits are believed to be the walls of rift valley complexes that developed as the continents separated²². In the Gulf of Mexico these thick salt deposits seem to lie on oceanic or greatly attenuated continental crust²⁷⁻²⁹. To a first approximation, they can be used to mark boundaries between the Palaeozoic crust of continental thickness and the developing Jurassic ocean basin (Fig. 1). This simplifying assumption requires the removal of the coastal plains and shelves of Texas, Louisiana and Mississippi and places the pre-Mesozoic crustal margin of North America 200-300 km inland of the present shorelines of Texas and Louisiana (ref. 28, Fig. 3). The hinging of younger deposits over this margin is expressed as a fault zone that stretches from Mobile, Alabama, to San Antonio, Texas²⁹.

The remaining pre-Mesozoic crustal margins around the Gulf can also be delineated by the distribution of evaporites. The western margin of the Yucatan Block in the Isthmus of Tehu-

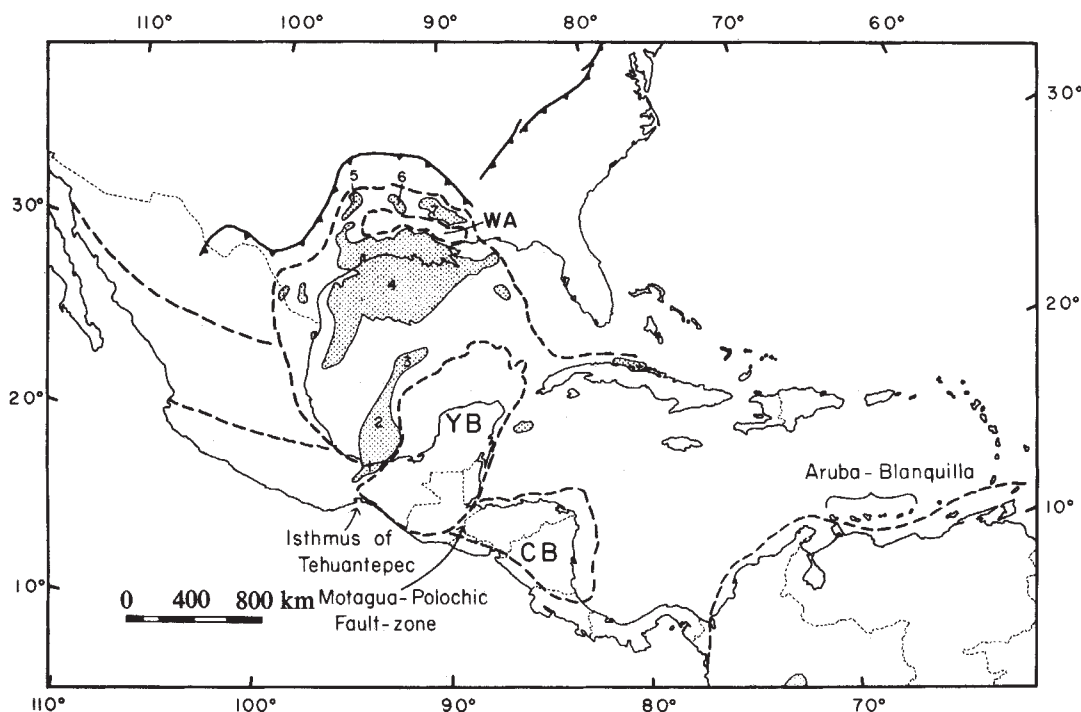


Fig. 1 Map of the Gulf of Mexico and Caribbean Sea showing limits of pre-Mesozoic continental crust (dashed line). YB, Yucatan Block; CB, Chortis Block; WA, Wiggins Arch; 1, Isthmian Basin; 2, Campeche Knolls; 3, Sigsbee Knolls; 4, Gulf Coast Salt Dome Province; 5, East Texas Salt Basin; 6, North Louisiana Salt Basin; 7, Mississippi Salt Basin. Stippling indicates areas of diapiric salt.

antepec is approximately coincident with the eastern edge of the Isthmian Salt Basin, Campeche Knolls and the western limit of Palaeozoic granitic rocks of the Chiapas Mountains near the western border of Chiapas, Mexico (ref. 29, Fig. 1). Seismic reflection studies across the Campeche and Florida Escarpments clearly show pinching out of the Jurassic–Cretaceous (?) Challenger unit (containing the evaporites) against older rocks that form the basement to these shelves^{5,30}. These studies and the absence of diapiric salt landward of the Campeche and Florida Escarpments indicate the continental shelves of Yucatan and Florida are underlain by pre-Mesozoic continental crust. Therefore, the Campeche and Florida Escarpments are taken to approximate the Palaeozoic continental crustal margin north and west of Yucatan and Florida respectively (Fig. 1). As shown in Fig. 1, Mexico was segmented into blocks as proposed by Schmidt and Anderson¹⁵.

Determination of the limits of pre-Mesozoic continental crust around the Caribbean is not as straightforward as in the Gulf of Mexico because of the paucity of ocean-opening salts and extensive post-Palaeozoic arc tectonics at the edges of the Caribbean plate. However, most of the circum-Caribbean continental masses are post-Palaeozoic in age, and therefore, only the margins of South America and the Chortis block (Honduras, portions of Guatemala and Nicaragua) need to be considered. The northern margin of South America was formed by rifting in the late Triassic and early Jurassic and experienced intense convergent and strike-slip related deformation after this time¹⁰. Nonetheless, analysis of the evolution of this margin in Venezuela by Maresch²⁴ justifies approximating the limits of pre-Mesozoic continental crust between the mainland and the Aruba–Blanquilla Island Chain (Fig. 1).

Two main post-Palaeozoic constructions alter the margins of the Chortis block and are removed in this reconstruction. These are the Nicaraguan Rise, which is a late Mesozoic island arc³¹ and the Cenozoic Middle America Arc along the Pacific coast of Guatemala, El Salvador and Nicaragua (Fig. 1). The Motagua–Polochic fault zone marks both the northern boundary of the Chortis block and the southern boundary of the Yucatan block. The eastern and southern limits of the Chortis block are unknown because they are buried under shelf sediments and Tertiary volcanics, but for this reconstruction the eastern limit is approximated by the 1,000-m isobath and the southern limit is approximated by projecting the trend of this isobath across Central America (approximately coincident with the southern Nicaraguan border).

The peri-Gulf and Caribbean blocks, now refined to their pre-Mesozoic shapes, can be assembled as shown in Fig. 2. In making this late Permian–early Triassic assembly opposing margins were matched when possible by closing correlative salt basins. Without this constraint, pre-Mesozoic margins were placed to provide the best morphological and geological fit. Application of this principle to the Gulf of Mexico indicates the extensive salt deposits west and north of Yucatan (Isthmian Basin, Campeche Knolls and the Sigsbee Knolls) correspond in age and extent to those of the northwestern margin (Gulf Coast Salt Dome Province). It is believed these were opposing margins of the developing Jurassic ocean^{22,23}. Good morphological agreement of pre-Mesozoic continental boundaries determined from salt distribution not only fixes the relative position of the Yucatan block to the southern margin of North America (Fig. 2), but also justifies the method of margin approximation described earlier. The Wiggins Arch, believed to be a pre-Mesozoic continental horst, is placed north-west of its present position against the North American Palaeozoic margin by closing the Mississippi, North Louisiana and East Texas Salt Basins. The wedge-shaped gap that remains between Yucatan and Florida can most easily be filled by placing the southeastern margin of the Chortis block against the Florida Escarpment.

Positioning the Yucatan and Chortis blocks in this manner entirely fills the gap between North and South America that is produced by the Atlantic reconstructions of LePichon and Fox⁸ and Sclater *et al.*²⁵. The small elongate gaps south of Florida and

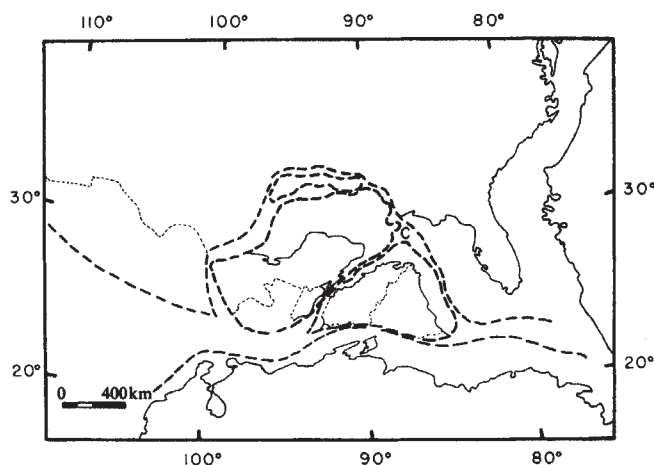


Fig. 2 Reconstructed positions of the continents around the Gulf of Mexico and Caribbean Sea during the early Triassic. C, Location of pre-Mesozoic portions of Cuba.

Yucatan (Fig. 2) may represent continental crust obliterated during the Bahama–Cuba and Motagua Collisions respectively. The remaining portions of Mexico must be displaced north-westwards of their present position before the opening of the Gulf. Whether or not this was accomplished by displacement along the Mohave–Sonora shear zone and the site of the Mexican volcanic zone (ref. 15, Fig. 1) or some other boundary must await further study. Palaeomagnetic data from Mexico and Central America³³ are difficult to interpret because of extensive post-Jurassic deformation in these regions. Pre-Mesozoic portions of Cuba are assumed here to be small and, therefore, do not alter the positions of the major blocks, but the present position of Cuba relative to the Yucatan and Chortis blocks suggests placing this continental crust at the junction of these blocks with the North American margin (area C in Fig. 2).

Discussion and implications

This reconstruction satisfactorily explains many features observed around the Gulf and Caribbean region. Most notably it explains the late Triassic to early Jurassic rifting event seen on the margins of the Gulf of Mexico and northern South America without juxtaposing North and South America and without leaving large gaps between these two continents. The Triassic La Quinta and correlative redbeds of Venezuela and Colombia and the early Jurassic Apoteri tholeiitic basalt flows of Guyana and Brazil³⁴ suggest that the Triassic graben complex associated with the Gulf–Atlantic opening extended into South America; but the subsequent seafloor spreading that occurred in some of these graben to open the oceanic basins between North and South America was not synchronous. Continuity of the Challenger seismic unit across the central Gulf^{5,29} indicates that seafloor spreading in the Gulf ceased at least by the end of Challenger deposition. Therefore, the Gulf was largely created in Lias–Dogger times. However, subsidence of the northern margin of South America which began in the late Jurassic²¹ suggests seafloor spreading in the Caribbean began in Malm times and continued into the Cretaceous.

The presence of extensive ocean-opening evaporites in the Gulf of Mexico and the paucity of evaporites in the Caribbean area may be explained by this geometry and timing of basin development. Figure 2 suggests that Mexico and Florida served as structural barriers against open ocean circulation in the Gulf as the Yucatan and Chortis blocks moved away from North America until Medial Jurassic times. At this time, communication with the developing Atlantic Ocean was established through the old Bahama channel and extensive evaporite deposition ceased in the Gulf. Apparently no such barriers restricted circulation in the developing Caribbean which was in

constant communication with the Pacific and Atlantic Oceans as it opened.

This reconstruction also suggests that the Palaeozoic magmatic arc resulting from closure of the Ouachita Ocean to form the Ouachita Mountains is likely to be found as the basement to Mesozoic sediments in Yucatan. Discovery of rhyolite of Silurian age showing a Mississippian metamorphic event (collision?) in the Yucatan No. 1 well of the Central Yucatan Peninsula³⁵ supports this view. I suggest that the granites and volcanic rocks that underlie Lower Jurassic (?Triassic) redbeds of Yucatan described by Lopez-Ramos³⁶ may also belong to this arc system. This arc was probably the source of middle Palaeozoic granitic and rhyolitic clasts and andesite tuffs in the Upper Palaeozoic flysch sequences of the Ouachitas³⁷.

Further support for this configuration is found in the Palaeozoic rocks of northeastern Mexico. The pre-Mesozoic schist, metaquartzite, granite and Devonian gneiss of eastern Coahuila and Nuevo Leon, cannot be correlated with Palaeozoic terrains in Chihuahua, Mexico, or the Ouachita belt in the southern US³⁷, but these rocks are remarkably similar to the pre-Mesozoic schist, granite and gneiss terrains of the Chiapas Mountains of the Isthmus of Tehuantepec²⁵. I suggest that these terrains were contiguous during the Palaeozoic (Fig. 2).

The pre-Mesozoic rocks (predominately phyllite, marble and schist)³⁵ of the Chortis block are not easily correlated with others in the Gulf or Caribbean region and its position in this reconstruction is largely based on morphology. However, phyllite and marble dredged from the Yucatan Channel near the

north-east corner of the Yucatan Peninsula³⁸ and schist found in the Basil Jones No. 1 well in Belice³⁶ are possible correlatives and as such they support location of the Chortis block as proposed in Fig. 2.

Correlation of pre-Mesozoic terrains between northern South America, the Yucatan block and the Chortis block is difficult because of the complex history of the northern South American margin. In general, Upper Palaeozoic rocks are restricted to a smooth curvilinear belt that extends from the Appalachians into the Andes, but these correlations are too crude to fix precisely the position of South America. Nevertheless, continuity of Palaeozoic terrains, good morphological agreement between South America and the other continental blocks (Fig. 2), and the Mesozoic tectonic history of northern South America^{10,21} support this reconstruction.

The margins of the Yucatan, Chortis and Mexican blocks probably originated as intracontinental transform fault zones that were coeval with the collision of Laurasia and Gondwanaland. Continued crustal shortening after collision probably caused shuffling of these blocks resulting in the complex late Palaeozoic to early Mesozoic deformation in Mexico and Central America as suggested by Dengo³⁵. I thank K. C. Burke, S. E. DeLong, J. F. Dewey, P. J. Fox, W. S. F. Kidd, R. E. Livaccari, A. M. C. Sengör and J. B. Stroup for useful suggestions, R. Carosella for assistance in preparing this paper, and Kevin Burke and Bill Kidd for helpful discussions. This work was supported by NSF grants EAR 7514254 and EAR 7803319 awarded to Kevin Burke.

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Abelson murine leukaemia virus protein is phosphorylated *in vitro* to form phosphotyrosine

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The Abelson murine leukaemia virus protein (P120) can become phosphorylated in vitro by $[\gamma\text{-}^{32}\text{P}]\text{ATP}$. The protein has been purified from cell membranes to the point that in specific conditions virtually all of the incorporated ^{32}P is in P120. The reaction is stimulated by Mn^{2+} and Mg^{2+} but not Ca^{2+} and is very rapid even at 0°C . The phosphate is linked to P120 at tyrosine, a linkage not previously reported for a phosphorylation reaction. Phosphorylation may be involved in the transforming activity of viruses that cause leukaemia as well as sarcomas.

ABELSON murine leukaemia virus (A-MuLV) is a defective retrovirus that causes a thymus-independent leukaemia^{1,2}. The leukaemic transformation can be carried out in cultures of bone marrow, fetal liver or spleen cells and many of the resultant cell lines have the characteristics of pre-B-lymphocytes³.

Continuous lines of fibroblastic cells can also be transformed by the virus⁴.

The A-MuLV genome is a hybrid consisting of about 25% of the genome of Moloney murine leukaemia virus (M-MuLV) flanking an insert of 3.6 kilobases of sequence that is homolo-

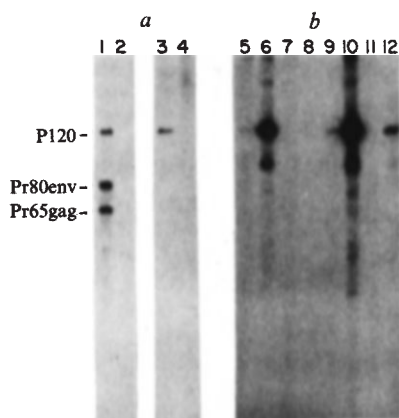


Fig. 1 Phosphorylation of P120 in an immunoprecipitate. *a*, 2M3/M cells (an A-MuLV-transformed BALB/c lymphoid cell line superinfected with Moloney-MuLV⁷) were labelled with ³⁵S-methionine (2.5×10^6 cells, $100 \mu\text{Ci}$ ³⁵S-methionine in 3 ml Dulbecco's minimal essential medium minus methionine for 1 h). Cells were extracted and clarified for immunoprecipitation^{7,9}, then one half was reacted with 5 μl anti-A-MuLV tumour serum⁹ (lane 1) and one half with 5 μl normal mouse serum (lane 2). Precipitates were collected with *S. aureus*, denatured and analysed on a SDS 10% polyacrylamide gel developed by fluorography^{25,26}. An equal number of unlabelled 2M3/M cells was extracted and clarified as above and immunoprecipitated with anti-A-MuLV tumour serum (lane 3) or normal mouse serum (lane 4). The precipitates were washed with 20 mM Tris-HCl, pH 8.0, by centrifugation, and resuspended in 50 μl of 20 mM Tris, pH 8.0, 10 mM MgCl₂, containing 1 μCi [γ -³²P]ATP (NEN, $2,300 \text{ Ci mmol}^{-1}$) for 10 min at 30 °C, washed, denatured and analysed by electrophoresis as described above. *b*, For each lane, 1×10^6 2M3 cells (an A-MuLV transformed lymphoid non-producer cell line) were extracted and clarified, then immunoprecipitated with 5 μl of a polyvalent goat anti-M-MuLV virion serum⁹. Individual precipitates were tested for phosphorylation of P120 as described above, with the following cations present: lane 5, 1 mM CoCl₂; lane 6, 10 mM CoCl₂; lane 7, 1 mM CaCl₂; lane 8, 10 mM CaCl₂; lane 9, 1 mM MnCl₂; lane 10, 10 mM MnCl₂; lane 11, 1 mM MgCl₂; lane 12, 10 mM MgCl₂.

gous to the DNA of normal mouse cells^{5,6}. Only a single protein of the A-MuLV genome has been identifiable using a wide range of sera; in the prototype A-MuLV strain, it is called P120 and represents a fusion of the N-terminal segment of molecular weight (MW) 30,000 of the M-MuLV gag protein precursor to protein of MW 90,000 that is non-viral^{7,8}. An antiserum specific for the non-MuLV-related portion of P120 has been prepared and reacts with protein of MW 150,000 in normal mouse cells^{9,10}. Thus, the non-viral portion of the P120 is closely related to a normal cell protein and is encoded by information that has at least partial homology to normal cell DNA.

Because no conditional mutants of A-MuLV are known, it has not been possible to prove that the P120 is the viral transforming protein, but because it is the only defined product of the genome and because of its association with A-MuLV-induced transformed cells, it has been assumed to be responsible for transformation by A-MuLV^{2,3}. The antiserum that recognises the non-M-MuLV-related portion of the P120 also reacts with the external surface of the plasma membrane of A-MuLV-transformed cells; thus, the P120 seems to have a portion exposed outside the cell⁹. Anti-M-MuLV sera do not react with the surface of A-MuLV-transformed, non-producer cells, indicating that the M-MuLV gag determinants are inside the cell. The protein therefore seems to be a transmembrane protein of the plasma membrane. P120 is not detectably glycosylated and is not cleaved by protease treatment of live cells; most of the polypeptide is therefore probably not exposed to the outside of the cell.

P120 is phosphorylated⁷. This observation led us to examine whether its properties might be related to those of the Rous

sarcoma virus transforming protein, pp60 src. That protein, which is recovered as a phosphoprotein from infected cells, has been shown to catalyse the incorporation of ³²P from [γ -³²P]ATP into the heavy chain of immunoglobulins that bind to it^{11,12}. The original demonstration of phosphorylation by pp60src was carried out with immunoprecipitates bound to *Staphylococcus aureus* and we therefore began our studies with such a system.

P120 phosphorylation in immunoprecipitates

To examine P120 for phosphorylation activity, an immunoprecipitate was incubated with [γ -³²P]ATP essentially as described by Collett and Erikson¹¹ for the Rous sarcoma virus transforming protein. Lysates were prepared from ³⁵S-methionine-labelled or from unlabelled A-MuLV-transformed lymphoid cells (2M3/M) (the cells also contained M-MuLV proteins because they were superinfected with M-MuLV). The extracts were mixed with control serum or antiserum directed

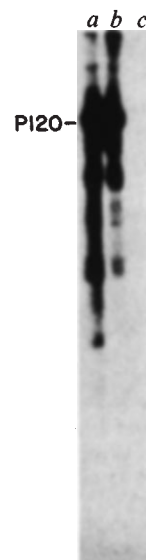


Fig. 2 Preparation and specificity of a soluble system that incorporates phosphate into P120. A frozen pellet of 2×10^9 2M3 cells was extracted at 0–4 °C with a detergent extraction mix of 100 ml of 10 mM NaH₂PO₄–Na₂HPO₄, pH 7.5, 100 mM NaCl, 1.0% Triton X-100, 0.5% Na deoxycholate, 0.1% SDS, 10% glycerol, 1 mM EDTA and 5 mM phenylmethylsulphonyl fluoride. This was clarified at 20,000 r.p.m. for 2 h in a Sorvall RC-5 refrigerated centrifuge. To the supernatant fluid was added 20 ml packed volume of DEAE-cellulose in the same buffer. The supernatant was recovered by centrifugation and then batch absorbed to 20 ml packed volume of phosphocellulose. P120 binds to phosphocellulose in these conditions as monitored by immunoprecipitation of ³H-leucine-labelled cellular lysates (data not shown). The resin was washed with the extraction buffer and P120 eluted with 30 ml of 0.5 M NaCl in extraction mix. The eluted material was dialysed against 10 mM KH₂PO₄–K₂HPO₄, pH 8.0, 100 mM NaCl and 25% glycerol. The dialysate was reconcentrated by absorption to phosphocellulose on a small column (1.2 × 10 cm) and elution into 4 ml of 0.5 M NaCl extraction buffer minus the SDS, containing 25% glycerol. This preparation represented 3% of the total protein in the original lysate and the recovery of P120 (estimated from experiments using labelled cellular lysates) was about 80%. This preparation was stable for over 6 weeks when stored at –20 °C. The enzyme preparation (5 μl) was assayed in a 50- μl reaction mix containing 20 mM Tris HCl, pH 8.0, 10 mM MnCl₂ and 1 μCi [γ -³²P]ATP for 10 min at 30 °C. One portion was analysed by electrophoresis to display all the phosphorylated proteins (lane *a*). An equal portion was immunoprecipitated with 5 μl of goat antiserum to total M-MuLV virion proteins (lane *b*; as in Fig. 1 and refs). A third equal portion was treated with 5 μl of normal goat serum (lane *c*). Analysis on SDS 10% polyacrylamide gel and autoradiography as in Fig. 1.

towards the A-MuLV-specific region of the P120 protein as well as the helper virus proteins. Immunoprecipitates were collected on fixed *S. aureus* immunoabsorbant. The precipitates from unlabelled cells were incubated with [γ - 32 P]ATP and Mg^{2+} for 10 min at 30 °C and washed. The 35 S-labelled samples and 32 P-labelled samples were then denatured and analysed by SDS-polyacrylamide gel electrophoresis. The 35 S-labelled sample had, as expected from previous work^{7,9}, a strong band of P120 precipitated by immune but not normal serum (Fig. 1a, lanes 1, 2). The 32 P-labelled precipitates also showed a band of radioactivity at MW 120,000 when precipitated by the immune but not the normal serum (Fig. 1a, lanes 3, 4). This experiment has been carried out with a variety of antisera directed at the gag or A-MuLV-specific regions of the P120 (refs 7, 9), and with a variety of A-MuLV-transformed cells that lacked the M-MuLV proteins, and labelling of the 120,000-MW protein has always occurred. Thus, the 32 P-labelled protein has the immunological as well as the electrophoretic characteristics of P120 and therefore seems to be P120 itself. No labelling of immunoglobulins was evident nor was there labelling of the M-MuLV proteins Pr65gag and Pr80env that were present in the immunoprecipitate (Fig. 1a, lane 3).

Table 1 Kinetic stability of the phosphate covalently bound to P120

Cation	First incubation		Second incubation	
	[ATP]	c.p.m. $\times 10^{-3}$	[ATP]	c.p.m. $\times 10^{-3}$
Mg	10 nM	21.2	10 nM	17.9
	10 nM	21.2	500 μ M	15.6
	500 μ M	1.6		ND
Mn	10 nM	63.1	10 nM	59.7
	10 nM	63.1	500 μ M	56.4
	500 μ M	2.8		ND

All reactions were carried out at 30 °C for 10 min in 20 mM Tris, pH 8.0, containing Mg or Mn at 10 mM in 50 μ l final volume using 10 μ l of phosphocellulose-purified enzyme. The first incubation contained either only radioactive [γ - 32 P]ATP (NEN, 2,400 Ci mmol⁻¹) at 10 nM final concentration or the same amount of radioactive ATP plus added unlabelled ATP to 500 μ M final concentration. The total c.p.m. incorporated was determined by cold 5% trichloroacetic acid (TCA) precipitation. For the second incubation, duplicate reactions from the first set of incubations using the 10 nM ATP condition were reincubated (10 min, 30 °C) with no additional ATP or with unlabelled ATP to 500 μ M final concentration and c.p.m. incorporated determined as above. ND, Not determined.

To examine the cation specificity of 32 P incorporation, different ions were tested at 1 and 10 mM. Mn^{2+} and Co^{2+} were most effective, Mg^{2+} was less effective and Ca^{2+} supported no detectable incorporation (Fig. 1b). In all cases where incorporation was seen, 10 mM cation was preferable to 1 mM. Ca^{2+} added to Mn^{2+} did not inhibit incorporation (data not shown). These effects were similar over an ATP concentration range of 20 nM–1 mM.

A variety of other variables were examined and their effects monitored semi-quantitatively by estimating band intensities following electrophoresis. [γ - 32 P]GTP was found to be a 32 P donor to P120 but at much lower efficiency than [γ - 32 P]ATP. Labelling with [γ - 32 P]ATP (at 10–20 nM) was complete within about 1 min even at 0 °C and the yield was about the same at 37 °C or 0 °C. Variation of the pH from 6 to 9 had little effect. No effect was noted when cyclic AMP, cyclic GMP or any of the four ribonucleoside monophosphates or diphosphates was added at 10–500 μ M. When 10–50 μ M of any of the four ribonucleoside triphosphates was added to 10 nM [γ - 32 P]ATP in the presence of Mg^{2+} , a threefold stimulation of incorporation of 32 P into P120 was seen. This effect is most remarkable for ATP because ATP will directly dilute the specific activity of the

[γ - 32 P]ATP. The result may imply a regulatory role for nucleoside triphosphates (NTPs) in the reaction. Less stimulation by NTPs occurred in the presence of Mn^{2+} .

A soluble system for P120 phosphorylation

Because the behaviour of P120 in immunoprecipitates might be misleading, we have developed a partial purification scheme for P120 starting with a detergent extract of infected cells. The purification was monitored using 3 H-leucine-labelled extracts and immunoprecipitation with specific antiserum as in Fig. 1, lane 1. P120 did not bind to DEAE-cellulose but bound to phosphocellulose and could be eluted at about 0.5 M NaCl. In the crude extract as well as in the phosphocellulose-purified material, 32 P incorporation from [γ - 32 P]ATP into P120 could be demonstrated by immunoprecipitation after the reaction. After phosphocellulose purification, as much as 85% of the acid-insoluble 32 P could be immunoprecipitated. At that stage, the electrophoretic profiles of equal amounts of the total reaction product (Fig. 2, lane a) and the immunoprecipitated product (Fig. 2, lane b) were quite similar. No radioactive bands were evident when normal serum was used in place of the immune serum (Fig. 2, lane c), although about 5% of the incorporated 32 P appeared in the precipitate after treatment with normal serum. The various labelled bands other than P120 that were precipitated by immune serum probably represented labelled degradation products of P120 that were produced during the incubation. This degree of specific phosphorylation by the phosphocellulose fraction has been confirmed in three separate preparations and a wide variety of reaction conditions.

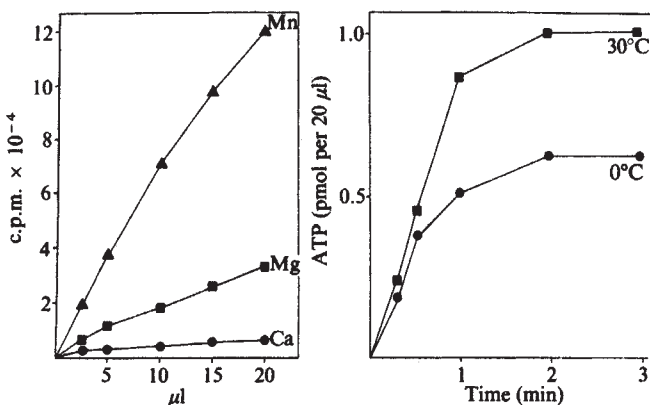


Fig. 3 Properties of the soluble P120 phosphorylation reaction. a, Varying amounts of an enzyme preparation prepared as described in Fig. 2 legend were reacted for 10 min at 30 °C in a final 50 μ l volume containing 1 μ Ci [γ - 32 P]ATP, 20 mM Tris, pH 8.0, and 10 mM $CaCl_2$ (○), $MgCl_2$ (□) or $MnCl_2$ (Δ). Labelled proteins were precipitated with 1 ml of cold 5% TCA, collected and washed by Millipore filtration and counted in 5 ml of Bray's solution. b, An enzyme preparation (10 μ l) was reacted in 50 μ l final volume containing 50 μ M ATP, 10 mM $MnCl_2$ and 20 mM Tris, pH 8.0, at 0 °C or 30 °C for the times shown. Reactions were stopped by addition of cold 5% TCA, collected and counted as above. Longer times of reaction (5–30 min) showed no increase above the 2-min level (data not shown).

Although this fraction is enriched for P120, analysis of its total protein content by Coomassie blue staining of SDS-polyacrylamide gels showed more than 50 separate bands of varying intensity (data not shown). P120 was so minor a component that we could not identify a specific band of P120 protein in this mixture.

Characterisation of the soluble phosphorylation reaction

Because the majority of ^{32}P incorporated by the phosphocellulose fraction was incorporated into specifically immunoprecipitable material, the properties of this fraction were investigated further using an acid precipitation assay. The yield of the incorporation was a linear function of the concentration of added protein but, as in the immunoprecipitate reaction, Mn^{2+} was greatly preferred over Mg^{2+} and Ca^{2+} was virtually inactive (Fig. 3a). The reaction yield was a function of the ATP concentration and was half maximal at about $10\text{ }\mu\text{M}$. At $50\text{ }\mu\text{M}$ ATP, the reaction showed a rapid time course at either 0°C or 30°C but at 30°C 30–40% more incorporation was evident than at 0°C (Fig. 3b). Cyclic AMP or cyclic GMP did not affect the reaction (data not shown).

Because sufficient P120 could be added to incorporate ^{32}P corresponding to about 10–15% of added $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ into acid-precipitable material, the fate of the substrate was examined. Preliminary experiments showed that at 30°C ATPase and phosphatase activities in the phosphocellulose eluate, possibly unrelated to P120, degraded much of the added ATP. At 0°C and with Ca^{2+} added, these were suppressed without affecting P120 labelling and therefore these conditions were used for the experiments. Equal amounts of enzyme were incubated at 0°C for 15 min with equal molar amounts of either $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ (Fig. 4, lanes a–c) or $[\alpha\text{-}^{32}\text{P}]\text{ATP}$ (Fig. 4, lanes d–f) using Ca^{2+} (lanes a, d), Mn^{2+} (lanes b, e) or Mn^{2+} and Ca^{2+} (lanes c, f); portions of the reactions were analysed by ascending chromatography. With Ca^{2+} alone, some degradation of both $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ to P_i and $[\alpha\text{-}^{32}\text{P}]\text{ATP}$ to ADP/AMP was evident but with Mn^{2+} present much more ADP was found than in its absence. Also, when Mn^{2+} was added, appreciable radioactivity from $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ became protein bound and remained at the origin. Approximately the same fractions of the ^{32}P in $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ became protein bound as the fraction of $[\alpha\text{-}^{32}\text{P}]\text{ATP}$ that was converted to ^{32}P -ADP. Thus, only the γ -phosphate of ATP seemed to participate in the labelling of P120, and ADP was released.

To examine whether the ^{32}P incorporated into P120 was turning over during the reaction, the $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ (10 nM) was diluted with a great excess of unlabelled ATP ($500\text{ }\mu\text{M}$) after 10 min of reaction and another 10 min of incubation was carried out (Table 1). With either Mg^{2+} or Mn^{2+} present, little loss of radioactivity was evident during the second incubation, although the excess of added ATP was sufficient to reduce the initial incorporation of ^{32}P by 10- to 30-fold. Thus, the phosphate incorporated in P120 was not subsequently released as acid-soluble products.

Identification of the P120-phosphate bond as phosphotyrosine

As an initial characterisation of the bond between the protein and the phosphate, the acid and alkali stabilities of the product were studied (Table 2). Neither 0.1 M HCl nor 0.1 M NaOH released any acid-soluble radioactivity after 30 min at 37°C . Even 1 M HCl at 37°C released no detectable ^{32}P , but 2 M HCl at 100°C for 20 h converted all the protein-bound ^{32}P to inorganic phosphate. These properties were inconsistent with the acid lability of phosphate linkages to nitrogen¹³ and the general lability of acylphosphate linkages¹⁴. Furthermore, the 2 M HCl hydrolysis should have released some phosphoserine or phosphothreonine if they were present¹¹.

All the radioactivity could be released from ^{32}P -P120 as $^{32}\text{PO}_4$ by treatment with calf intestinal phosphatase or bacterial alkaline phosphatase (Fig. 5). This cleavage could be inhibited by the addition of pure phosphomonoester compounds like phosphoserine (data not shown). In this experiment, the ^{32}P -P120 was predigested with chymotrypsin in an attempt to increase the sensitivity of ^{32}P -P120 to hydrolysis but in other

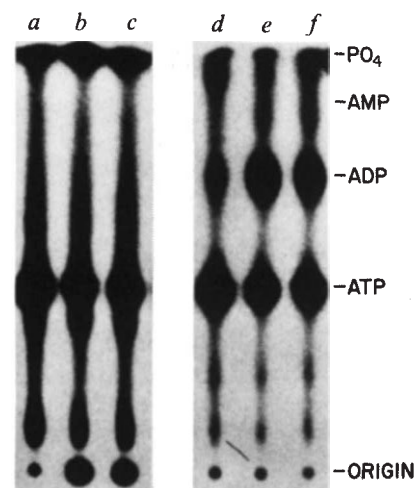


Fig. 4 Fate of ATP during the P120 phosphorylation reaction. Phosphorylation reactions ($100\text{ }\mu\text{l}$ final volume) contained $20\text{ }\mu\text{l}$ of enzyme preparation and either $1\text{ }\mu\text{Ci}$ of $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ (lanes a–c) or $[\alpha\text{-}^{32}\text{P}]\text{ATP}$ (lanes d–f). Both ATPs were adjusted to 600 Ci mmol^{-1} . Also present were 20 mM Tris, $\text{pH } 8.0$, and 10 mM CaCl_2 (lanes a, d), 10 mM MnCl_2 (lanes b, e) or 10 mM CaCl_2 plus 10 mM MnCl_2 (lanes c, f). Reactions were at 0°C for 15 min and were then diluted 20-fold into excess EDTA. Aliquots of $1\text{ }\mu\text{l}$ of each were analysed on polyethylenimine-coated thin layer plates (Brinkman, PEI 300) by ascending chromatography in $0.85\text{ M K}_2\text{HPO}_4$, adjusted to $\text{pH } 3.5$. Positions of ^{32}P - PO_4 and marker nonradioactive AMP, ADP and ATP (visualised under UV light) are shown.

experiments this has proved unnecessary. Thus, the bond between the ^{32}P and the protein behaved like a phosphomonoester.

To search for phosphomonoesters that were more labile to acid than phosphoserine or phosphothreonine, a preparation of ^{32}P -P120 from the *in vitro* phosphorylation system was hydrolysed at 100°C in 6 M HCl for 0, 2, 4 or 6 h and the products were separated by $\text{pH } 3.5$ electrophoresis (Fig. 6, lanes a–d). Before hydrolysis, the radioactivity remained at the origin but at all times of hydrolysis extensive production of free $^{32}\text{PO}_4$ was evident. Also evident after hydrolysis was a prominent spot co-migrating with a phosphotyrosine standard. The apparent

Table 2 Stability of the phosphate bond in *in vitro* phosphorylated P120

Treatment*	% Protein bound†	% Free PO_4 ‡
H_2O , 37°C , 30 min	100	ND
0.1 M HCl , 37°C , 30 min	99	ND
0.1 M NaOH , 37°C , 30 min	101	ND
1 M HCl , 37°C , 30 min	102	ND
H_2O , 0°C , 20 h	ND	< 5
2 M HCl , 100°C , 20 h	ND	> 95

* $8,000\text{ c.p.m.}$ of *in vitro* phosphorylated P120-P prepared and washed free of unincorporated $[\gamma\text{-}^{32}\text{P}]\text{ATP}$ as described in Fig. 6 legend was treated in $200\text{ }\mu\text{l}$ of the solution indicates.

† Samples were precipitated with cold 5% TCA, collected and washed on Millipore filters and counted in Bray's solution. The control is set at 100% .

‡ Following hydrolysis, the samples were concentrated by lyophilisation and analysed by high voltage electrophoresis at $\text{pH } 3.5$ as described in Fig. 6 legend. Autoradiograms with orthophosphate markers were used to locate the spot of free phosphate, which was excised and counted by Cerenkov radiation. ND, Not determined.

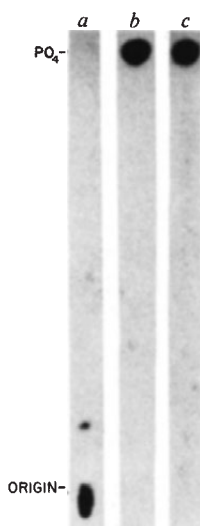


Fig. 5 Susceptibility of ^{32}P -P120 to phosphatase. *In vitro* phosphorylated P120 prepared in a soluble reaction (10 mM MnCl_2 , 1 μCi [γ - ^{32}P]ATP, 20 mM Tris, pH 8.0, 20 μl enzyme preparation, 0 °C, 10 min) was precipitated with cold TCA and washed with ethanol to remove unincorporated ATP. The pellet was resuspended in 100 mM NH_4HCO_3 , digested with α -chymotrypsin (10 $\mu\text{g ml}^{-1}$, 37 °C, 12 h), and then boiled for 5 min. Portions containing 2,500 c.p.m. were untreated (a), digested with calf intestinal phosphatase (0.01 units, Boehringer Mannheim) (b) or bacterial alkaline phosphatase (0.01 units, Worthington) (c) in 20 mM NH_4HCO_3 and 5 mM MgCl_2 for 30 min at 37 °C. Aliquots of 5 μl were analysed by high voltage electrophoresis (Savant) in pyridine acetic acid (pH 3.5) on Whatman 3-MM paper at 2,400 V for 1 h. The position of a ^{32}P - PO_4 standard is noted.

phosphotyrosine was eluted and chromatographed with an internal phosphotyrosine marker (Fig. 7). Phosphoserine and phosphothreonine migrated closer to the front than phosphotyrosine in this system. Trace amounts of a compound migrating with phosphoserine were also released by hydrolysis of this preparation (Fig. 6, lanes b–d) but recovery of phosphoserine has been variable and always small.

Phosphotyrosine is known to be more acid labile than either phosphoserine or phosphothreonine¹⁵. Thus, although the yield of ^{32}P -phosphotyrosine was never more than 40–50% of the input radioactivity in ^{32}P -P120, the virtual lack of phosphoserine and phosphothreonine, coupled with the sensitivity of all the ^{32}P to phosphomonoesterases (Fig. 5), is consistent with the interpretation that almost all ^{32}P in ^{32}P -P120 is actually in phosphotyrosine linkage. This report, and a recent independent observation on middle T antigen of polyoma virus²⁰, appear to represent the first direct demonstrations that phosphotyrosine can occur as a distinct entity in phosphoproteins, although three examples of a tyrosine-*O*-*P*-nucleotidyl linkage have been reported (refs 16–19 and J. Wang, personal communication). Although the occurrence of phosphotyrosine may represent a unique or very rare situation, the possibility that this linkage is commonly missed because of its acid lability should be considered.

P120 has previously been shown to be labelled in cells exposed to $^{32}\text{PO}_4$. To examine whether this *in vivo* phosphorylation occurs at tyrosine residues, *in vivo*-labelled ^{32}P -P120 was hydrolysed in acid using the same conditions as described for the *in vitro*-phosphorylated protein (Fig. 6, lanes e–h). The *in vivo* label was recovered mainly as phosphoserine or free phosphate. Virtually no phosphotyrosine was evident and the small spot that migrated just ahead of phosphotyrosine had too little radioactivity to be analysed further. It thus seems that most of the *in vivo* phosphorylation occurs at serine residues, but the extensive release of ^{32}P as inorganic phosphate could suggest that more labile bonds are also present. P120

contains the M-MuLV gag protein pp12 which is known to have serine residues that can be phosphorylated¹⁹; perhaps some or all the phosphoserine in the *in vivo*-labelled P120 is located in the pp12 region of the molecule.

Interpretation of the P120 phosphorylation reaction

The properties of the P120 phosphorylation reaction described here are unique and not easily interpretable. First, the linkage of phosphate to tyrosine is a unique one and thus offers no clue to its function. We have recently become aware that an apparent autophosphorylation of polyoma virus middle T antigen has also been shown to involve phosphotyrosine. Thus, phosphotyrosine is involved in more than one viral protein thought to play a part in transformation²⁰. Second, the reaction seems to be an autophosphorylation. Although it is difficult to be certain whether any other proteins are involved in the reaction, no protein other than P120 is present in the immunoprecipitates at even 10% of the level of P120 and yet rapid phosphorylation of P120 occurs in the immunoprecipitate even at 0 °C. The M-MuLV proteins (evident in Fig. 1, lane 1) are not involved because an immunoprecipitate from cells lacking M-MuLV proteins was active in P120 phosphorylation. Third, the rapid reaction even at 0 °C is suggestive of the formation of an intermediate in an enzyme reaction. The stability of the phosphate-protein linkage after dilution of the [γ - ^{32}P]ATP indicates that the reaction as it occurs is not catalytic phosphate transfer. It is, of course, quite possible that the protein kinase reaction is meant to produce a stable tyrosine phosphorylation but it is significant that P120 from cells labelled with ^{32}P - PO_4 had little or no phosphotyrosine.

One attractive possibility is that P120 is a phosphotransferase or phosphatase, but that in the assay conditions used here it is

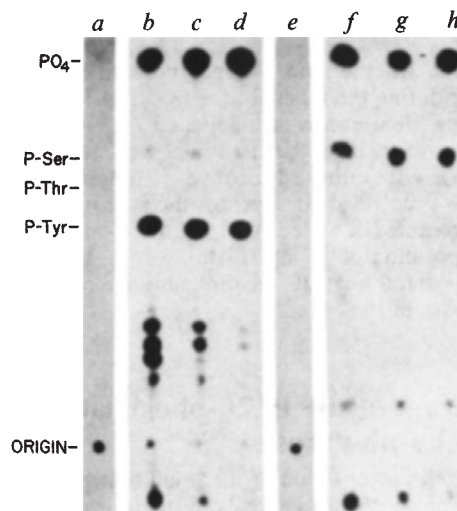


Fig. 6 Analysis of acid hydrolysates of phosphate-labelled P120 made *in vitro* and in cells. About 5,000 c.p.m. of *in vitro* phosphorylated P120 (0 °C, 10 mM MnCl_2 reaction conditions as for Fig. 3) recovered by immunoprecipitation, was washed with TCA and ethanol to remove unincorporated [γ - ^{32}P]ATP and was either left untreated (a) or hydrolysed with 6 M HCl at 100 °C, in a sealed ampoule for 2 h (b), 4 h (c) or 6 h (d). About 2,000 c.p.m. of *in vivo* phosphorylated P120 (2×10^5 2M3 cells labelled in phosphate-free medium with 200 μCi of ^{32}P - PO_4 for 3 h, lysed and immunoprecipitated as for Fig. 1, lane 1) was washed with TCA, ethanol and was either left untreated (e) or hydrolysed with 6 M HCl at 100 °C for 2 h (f), 4 h (g) or 6 h (h). Samples were lyophilised, resuspended in 5 μl water and a portion analysed by high voltage electrophoresis (pH 3.5) as in Fig. 5. The position of marker phosphoserine, phosphothreonine and phosphotyrosine¹⁵ was determined by ninhydrin staining.

unable to transfer the phosphate from its linkage to tyrosine. By this postulate, the P120 phosphorylation could be a partial reaction. Possibly, we need to find the appropriate substrate for phosphate transfer, but two other interpretations should be considered: (1) that removal of P120 from its normal association with membranes has prevented a second step that it ordinarily carries out; thus, we might trap an intermediate state. (2) P120 might initially form a bond other than phosphotyrosine but might transfer the phosphate to tyrosine because of an altered configuration due to its removal from membranes. The P120 is a fused product of viral information and part of a cellular gene; possibly the tyrosine is in the viral portion and is not normally available in the cellular product. We have previously reported that only extracts of A-MuLV-transformed cells could function *in trans* to label heat-inactivated A-MuLV protein of another strain when both were mixed before immunoprecipitation and phosphorylation assay²¹. Extracts of normal cells or cells transformed by other agents were ineffective. One possibility is that the active form for phosphorylation of P120 is a dimer or higher multimer of like subunits. Such preformed complexes would account for the rapid time course and allow for the rescue of heat-inactivated subunits by reforming complexes with native subunits provided *in trans*.

Comparison with Rous sarcoma virus pp60src

Although A-MuLV selectivity transforms lymphoid and occasionally other haematopoietic cells in infected animals, it will transform cultured fibroblastic cell lines^{3,4}. Thus, in culture, it can behave like a sarcoma virus and it is not too surprising that the P120 has some parallels with the Rous sarcoma virus protein (pp60src). That protein, like P120 (ref. 9), is membrane associated²², suggesting that transformation events may often take place at the cell surface. The A-MuLV protein is known to have a portion extending out of the cell because antisera that immunoprecipitate P120 also stain the exterior membrane of live, A-MuLV-transformed cells⁹. With pp60src, the antisera only label the internal surface of the plasma membrane but this could reflect differences in the determinants recognised by the available sera rather than fundamental differences in the organisation of the protein.

Another parallel between pp60src and P120 is that both are involved in phosphorylation reactions. The major activity of pp60src, however, is *trans*-phosphorylation of acceptor proteins (such as immunoglobulin, phosphatidyl). By contrast, P120 causes little or no labelling of added protein (data not shown) or of the immunoglobulin that binds to it. Whether this difference is fundamental or is a peculiarity of the specific systems is unclear but some phosphorylation of pp60src itself has been noted²³.

Although pp60src has not been reported to form phosphotyrosine, this question needs further investigation. Other properties of the pp60src and P120 reactions have similarities, the major one being that both reactions occur rapidly at 0 °C. Also, Ca²⁺ will support neither reaction but is not inhibitory to either one.

Richert *et al.*²⁴ have argued that pp60src is more like a nucleotide kinase than a protein kinase, although the only

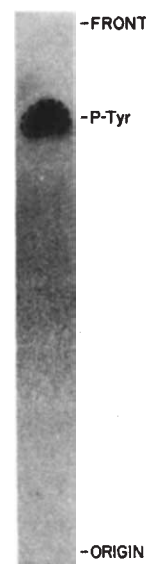


Fig. 7 Co-chromatography of phosphotyrosine with the major phosphorylated amino acid recovered from *in vitro* phosphorylated P120. Material from the prominent spot migrating on high voltage electrophoresis as phosphotyrosine shown in Fig. 6, lane *d*, was eluted with water, mixed with authentic phosphotyrosine, concentrated by lyophilisation and analysed by ascending chromatography on cellulose thin layer plates (Brinkman, CEL 300) in saturated ammonium sulphate: 1 M sodium acetate: isopropanol (40:9:1)²⁷. The dashed line shows the position of the ninhydrin-stained phosphotyrosine internal marker.

demonstrated activity of pp60src is protein kinase activity. As described above, P120 of A-MuLV also has properties that suggest its autophosphorylation activity may represent formation of an enzyme intermediate, although we would not single out nucleotide kinases as the best parallel.

In summary, both the Rous sarcoma virus protein, pp60src, and the A-MuLV protein, P120, are membrane-associated, phosphorylating proteins that show rapid reactions at 0 °C (refs 22, 24). Early proteins of SV40 and polyoma, two other transforming viruses, also are phosphorylated *in vitro* and at least one of these seems to be phosphorylated at a tyrosine residue²⁰. These similarities suggest that the leukaemogenic (and fibroblast transformation) activity of A-MuLV, the sarcomagenic activity of Rous sarcoma virus and the generalised transforming potential of DNA tumour viruses may have a similar basis.

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Note added in proof: T. Hunter and B. M. Sefton (*Proc. natn. Acad. Sci. U.S.A.*, in the press) and R. Erikson and colleagues (personal communication) have recently shown that the protein kinase activity associated with pp60src of Rous sarcoma virus specifically phosphorylates tyrosine residues.

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β -Chain contact sites in the haemoglobin S polymer

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The amino acid residues involved in the areas of contact that stabilise the haemoglobin S polymer fibre seem to be the same ones that stabilise the basic unit of the deoxyhaemoglobin S crystal: the Wishner-Love double strand. The haemoglobin S fibre is probably formed by a unique packing of these double strands.

ANALYSIS of the supramolecular structure of the deoxy-haemoglobin (deoxy Hb) S polymer has been attempted by diffraction of high resolution electron microscopy plates¹ and by X-ray crystallography of aligned fibres². A detailed description of the structure, however, must account for data about specific amino acid residues which alter the polymerisation. Our laboratory has approached this problem with a strategy that utilises binary mixtures of Hb S and Hb variants with mutations of residues at the molecular surface^{3,4}. Since the predominant species in such mixtures are hybrid tetramers of the type $\alpha_2\beta^*\beta^x$ or $\alpha\beta^*\alpha^x\beta^A$, their behaviour can show whether the mutated residue affects the polymerisation of Hb S. This article describes several residues at the surface of the tetramer that appear to be involved in areas of contact in the polymer and compares these to the contacts found in deoxy Hb S crystals by Love and associates⁵.

Isolation of mutants and other experimental procedures

Haemolysates were made from blood samples obtained after informed consent from donors with sickle cell anaemia (SS) diagnosed and characterised in our Heredity Clinic. These haemolysates were selected to contain less than 5% Hb F (measured as the alkaline-resistant fraction⁶) and were used without further purification. Hb Hope was obtained from a homozygous donor and contained less than 1% Hb F, and less than 2% Hb A₂ as measured by column chromatography⁷.

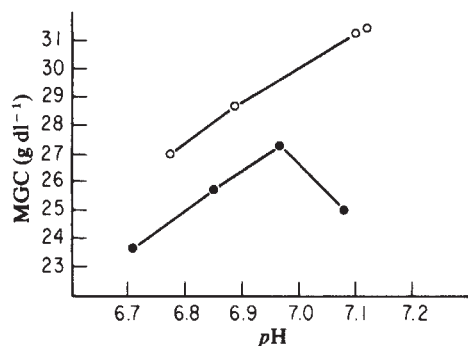


Fig. 1 Minimum gelling concentration (MGC) of Hb S (40%) + Hb A (60%) (○), and Hb S (40%) + Hb I Toulouse (60%) (●) at different pH. Hb I Toulouse when mixed with Hb S promotes gelation as compared to Hb A. Buffer: 0.15 M KPO₄, Temperature 24 °C.

The other haemoglobin variants used in these studies were isolated from haemolysates of heterozygotes' blood by chromatography on columns of DE-52 (Whatman) using 0.05 M Tris-HCl buffer with a pH between 7.5 and 8.2, depending on the haemoglobin, as described elsewhere in detail⁴. The characterisation of Hb Manhasset (β 139 Asn → Lys) will be reported separately⁸. All samples were concentrated and simultaneously dialysed against 0.15 M potassium phosphate (pH 7.35) and minimum gelling concentrations were determined at 24 °C as described previously⁹.

In some of the experiments we use dithionite to reduce methaemoglobin and/or to assure complete deoxygenation. The dithionite solution was prepared by mixing the powder anaerobically with 0.001 M NaOH. An appropriate aliquot of this solution was added anaerobically to the deoxygenated haemoglobin mixture. The final solution contained 1.2 M of dithionite per mol of haem and the final pH was consistently 6.9.

Rationale of the experimental design

We had previously proposed on the basis of indirect evidence⁹ confirmed by others¹⁰ that the two β -chains of Hb S behave unequally in the formation of the polymer. More recently, we obtained direct evidence¹¹ that only one of the β 6 valine substitution sites of the Hb S tetramer is actively involved in an area of contact. The symmetrical area in the other β^* chain is not involved in any area of contact¹². Due to the symmetry rela-

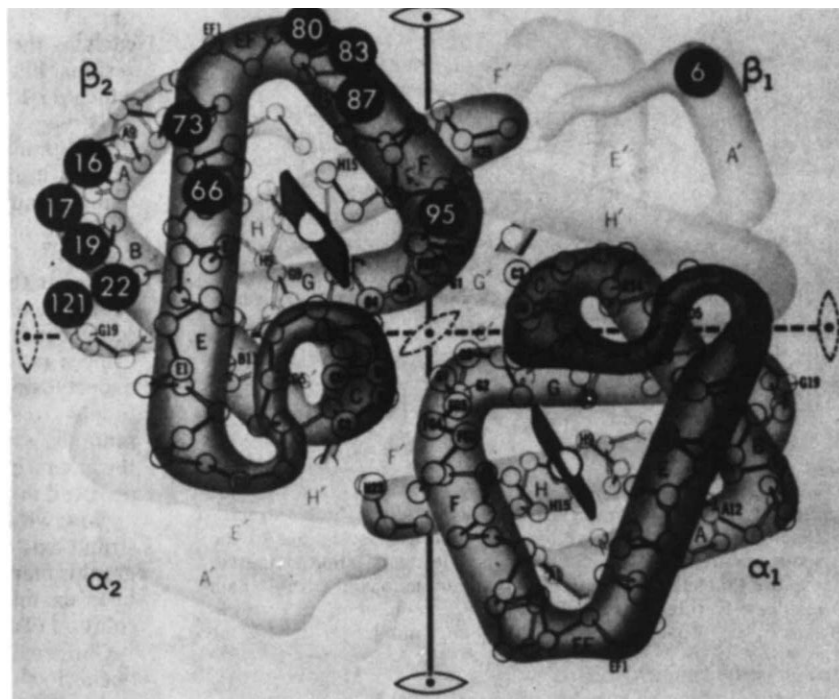
Table 1 Effect of β -chain mutations on the gelation of Hb S

Mutant	Site	Substitution	Hb S + Hb A* MGC (g dl ⁻¹)	Hb S + Hb X MGC (g dl ⁻¹)	Δ MGC	pH
J Baltimore	β 16(A13)	Gly → Asp	29.0	32.5	+3.5	6.8†
J Amiens	β 17(A14)	Lys → Gln	28.7	32.5	+4.0	6.9†
D Ouled Rabah	β 19(B1)	Asn → Lys	32.10	35.3	+3.2	7.1
E	β 26(B8)	Glu → Lys	32.4	33.2	—	7.1
J Lome	β 59(E9)	Lys → Asn	32.3	33.1	—	7.1
I Toulouse	β 66(E10)	Lys → Glu	29.4	28.9	—	6.8†
Pyrgos	β 83(EF7)	Gly → Asp	31.5	25.0	-6.5	7.1
Aganogi	β 90(F6)	Glu → Lys	32.1	35.1	+3.0	7.1
Detroit	β 95(FG2)	Lys → Asn	32.7	33.7	—	7.2
N Baltimore	β 95(FG2)	Lys → Glu	28.6	31.6	+3.0	6.9†
			32.0	38.5	+6.5	7.1
			29.5	37.0	+7.0	6.9†
Hofu	β 126(H4)	Val → Glu	35.3	34.6	—	7.1
K Woolwich	β 132(H10)	Lys → Gln	32.3	33.2	—	7.1
			29.2	29.8	—	6.8†
Hope	β 136(H14)	Gly → Asp	32.4	32.7	—	7.1
Manhasset	β 139(H17)	Asn → Lys	32.3	31.9	—	7.1

* Hb A was obtained from the same chromatographic separation in most cases.

† Deoxygenation with dithionite.

Fig. 2 Mutational sites (black circles with white numbers) that have been shown to interfere with the polymerisation of Hb S in solution. This diagram is a modification of a figure by Irving Geis. References for the mutations not reported here can be found in ref. 12. The diagram uses the nomenclature of Perutz for helical and nonhelical segments. White digits correspond to sequence numbers. Note that all mutational sites described correspond to the $\beta 2$ chain when $\beta 1$ is carrying the active 6-Val site.



tionships between the chains in the haemoglobin tetramer each β -chain has a different set of interactions with each of the α -chains. With one of the α -chains, a β -chain forms a highly stable system of strong hydrophobic and polar interactions resulting in a very stable $\alpha 1\beta 1$ dimer. The same $\beta 1$ chain forms weaker interactions with the $\alpha 2$ chain so that the $\alpha 1\beta 2$ interface is broken when the tetramer dissociates into dimers. These considerations highlight the need to define the effect of a surface residue specifically in terms of its activity in $\alpha 1$, $\alpha 2$, $\beta 1$, or $\beta 2$, in relation to the 'active' $\beta 6$ valine site.

To define β -chain interaction sites, we mix Hb S with the β -chain variant, Hb X (generally in the proportion of 40% Hb S and 60% Hb X). The predominant species in the mixture (because of the dimerisation of both parental tetramers and subsequent free rearrangement) is the hybrid $\alpha_2\beta^s\beta^x$. It is obvious that this allows us to measure the activity of the mutant residue located *trans* to the β -chain carrying the active $\beta 6$ Val substitution. In order to explore the effects of *cis* residues, Hb variants with two mutations in the same β -chains are required, one of which is identical to the Hb S substitution. Three such double mutants have been examined³. If the minimum gelling concentration of the doubly mutated Hb is abnormal, further information pertaining to the *cis* or *trans* character of the effect can be obtained by mixing this variant with Hb A and observing the behaviour of the hybrid $\alpha_2\beta^{s,x}\beta$.

Effect of several β mutations on Hb S polymerisation

The results obtained with the β -chain mutants are summarised in Table 1. Of the 14 mutants examined, 6 altered the polymerisation of Hb S. Mutations at sites $\beta 16$, $\beta 17$, $\beta 19$, $\beta 83$ and $\beta 95$ had an inhibitory effect, whereas the mutation at site $\beta 66$ facilitated polymerisation (Fig. 1), an effect similar to that found with substitutions at $\beta 121$ (Hb O Arab and Hb D Los Angeles)^{13,14}. It should be emphasised that the assignment of these residues to areas of interaction pertain exclusively to the $\beta 2$ chain *trans* to the $\beta 1$ chain designated as the one carrying the active 6-Val site. The effects of the corresponding *cis* residues in the sequence of the $\beta 1$ chain remain to be defined. The magnitude of the alterations of gelation in mixtures with Hb S suggests that $\beta 66$ and the nearby $\beta 73$ site (previously studied)^{15,16} is part of an important single area of interaction between the tetramers of the polymer.

Figure 2 shows all the β -chain sites that have been implicated in areas of contact, including the ones reported here. Those that have been examined and found thus far not to participate are listed in Table 2.

Assigned sites of interaction and the Hb S crystal

Wishner and his associates⁵ have described the crystal structure of deoxy Hb S and found that the basic unit is a double strand stabilised by side-to-side and up-down interactions involving mainly the β -chains (Figs 3, 4). A salient feature of this structure is that only one of the β -chains has a 6-Val residue involved in a contact area. This is in accordance with our data on the formation of the Hb S polymer¹². The relevance of this structure to the deoxy Hb S fibre can be tested further by determining if other contacts found in the crystal structure can be shown to be active in polymerising solutions of deoxy Hb S. Of the sites examined thus far, $\beta 66$, $\beta 73$, $\beta 83$ and $\beta 87$, which were found to be involved in the side-to-side contact of the crystal, were also

Table 2 Sites shown tentatively *not* to interfere with the polymerisation of Hb S in solutions

	Site	Substitution	Ref
$\beta(2)$ <i>trans</i>	Deer Lodge	$\beta 2$ (His $\rightarrow$ Arg)	19
	G Makassar	$\beta 6$ (Glu $\rightarrow$ Ala)	19
	Leiden	$\beta 6$ (Glu $\rightarrow$ O)	20
	G San Jose	$\beta 7$ (Glu $\rightarrow$ Gly)	21
	Saki	$\beta 14$ (Leu $\rightarrow$ Pro)	22
	E	$\beta 26$ (Glu $\rightarrow$ Lys)	This article
	G Copenhagen	$\beta 47$ (Asp $\rightarrow$ Asn)	3
	C Ziguinchor	$\beta 58$ (Pro $\rightarrow$ Arg)	23
	J Lome	$\beta 59$ (Lys $\rightarrow$ Asn)	This article
	J Cairo	$\beta 65$ (Lys $\rightarrow$ Glu)	23
	J Chicago	$\beta 76$ (Ala $\rightarrow$ Asp)	3
	Aganogi	$\beta 90$ (Glu $\rightarrow$ Lys)	This article
	Alkylolation	$\beta 93$ (Cys)	19
	Hofu	$\beta 126$ (Val $\rightarrow$ Glu)	This article
	Woolwich	$\beta 132$ (Lys $\rightarrow$ Gln)	This article
	Hope	$\beta 136$ (Gly $\rightarrow$ Asp)	This article
	Manhasset	$\beta 139$ (Asn $\rightarrow$ Lys)	This article
	S Travis	$\beta 142$ (Ala $\rightarrow$ Val)	24
$\beta(1)$ <i>cis</i>	C Ziguinchor	$\beta 58$ (Pro $\rightarrow$ Arg)	23
	C Harlem	$\beta 73$ (Asp $\rightarrow$ Asn)	16
	S Travis	$\beta 142$ (Ala $\rightarrow$ Val)	24

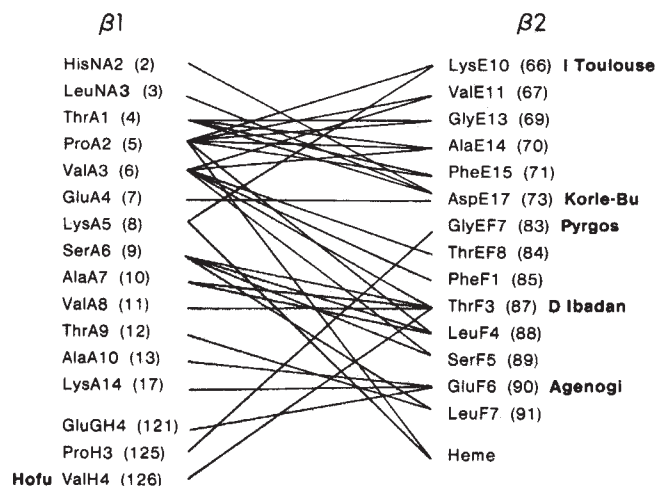


Fig. 3 Side-to-side contacts in the Wishner-Love double strand⁵. Lines connect residues within a 5 Å radius. Contiguous to the sequence site, we have indicated (in bold letters) the mutant used to explore that site. All the side-to-side interactions involve β -chain residues. Residues are identified by Perutz nomenclature and in parenthesis by the sequence number.

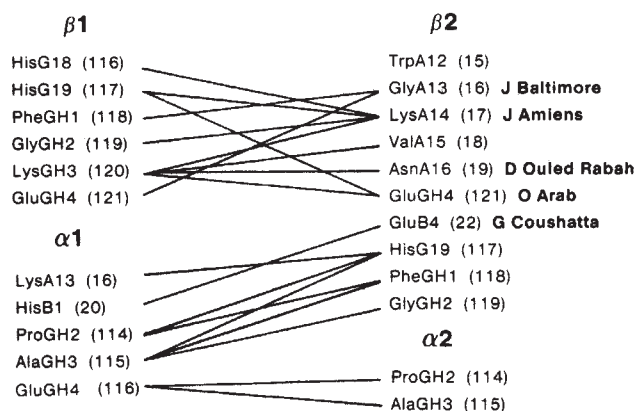


Fig. 4 Up-and-down contacts in the Wishner-Love double strand⁵. Lines connect residues within a 5 Å radius. Contiguous to the sequence site we have indicated (in bold letters) the mutant used to explore that site. Nomenclature as in Fig. 3.

found to have strong effects on the polymerisation of solutions of Hb S (Fig. 3). Note that these residues were shown to be part of the receptor site located in the $\beta 2$ chain of the crystal (the $\beta 1$ chain carries the 'active' $\beta 6$ -Val site). This, of course, is in complete agreement with our results, as our experimental design with Hb S-Hb X mixtures detects only the effects of the mutant β^* residues in the $\beta 2$ chain. A further interesting point can be made with regard to the residue $\beta 126$, that we have explored using Hb Hofu. Although $\beta 126$ -Val participates in the interac-

ting site of the crystal it is provided by the same ($\beta 1$) chain carrying the active 6-Val site. We do not find any effect of this residue, but this is not in contradiction with the crystal data, in which $\beta 126$ is not in an area of contact.

Three residues are not coincident with the crystal data. Residue $\beta 80$, implicated by the inhibitory effect of Hb Gifu⁴, is not present in the side-to-side contact area, but it is very close, as demonstrated by the fact that residue $\beta 83$ is involved. In addition, in the Hb F crystal, $\beta 80$ is featured in this area of contact¹⁷. The residue at $\beta 90$ is included in the side-to-side contact in the crystal, but we find that it is inactive in solution. It should be remembered, however, that this residue is at the edge of the contact area and interacting residues have been included using a radius of 5 Å (ref. 5) which is rather large relative to expected hydrogen bond distances and Van der Waals radii. Finally, residue $\beta 95$, which we have examined using two mutants, is not involved at all in the areas of contact between the tetramers in the crystal double strand. This residue could be involved in other contacts that are specific for the fibre.

Now we turn to the up-down interaction along the crystal strand axis (Fig. 4). Of the residues involved by the crystallographic map of deoxy Hb S, $\beta 16$, $\beta 17$, $\beta 19$, $\beta 22$ and $\beta 121$ have been examined. All of them have been found to be active in solution (Table 1, Fig. 2).

Conversely, of the 21 β -residues examined thus far that have been shown to be inactive in solution, 20 of them are not found in the areas of contact between the tetramers forming the double strands of the crystal (Table 2). The only exception was $\beta 90$, as noted above.

In terms of the α -chain sites, there are only five contact sites provided by $\alpha 1$ and two contact sites provided by $\alpha 2$ that stabilise the up-down contacts of the double strand in the crystal. Of these, only $\alpha 116$ has been examined by Benesch *et al.*¹⁸; but until it is established whether the effect found is attributable to the $\alpha 2$ or $\alpha 1$ chain, this data cannot be used to test the crystal relevance to the solutions of Hb S.

Conclusions

The data presented here show remarkable coincidence between the crystallographically defined contact sites for the double strands of deoxy Hb S and the residues that appear to be active in solutions undergoing polymer formation. This suggests that the double strand is the building unit in the assembly of the fibre. At first approximation the supramolecular structure proposed by Dykes *et al.*¹ could be accommodated with seven double strands as defined in the crystal.

It should be kept in mind that the crystal and fibre cannot be identical structures. It is likely that residues of the α chain involved in the stabilisation between double strands in the crystal are not significant for the fibre. The stabilisation of the double strands present in the fibre may involve interactions between the α -chains which are not present in the crystal. The definition of these α - α contacts will provide the evidence required to establish the packing order of the Wishner-Love double strand in the haemoglobin S fibre.

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Abnormal expression of chromosomal rabbit β -globin gene in *Saccharomyces cerevisiae*

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A 5.1 kilobase-pair segment of rabbit chromosomal β -globin DNA was joined to pJDB219, a plasmid consisting of pMB9, the 2- μ yeast plasmid and the yeast *leu-2* gene. *Saccharomyces cerevisiae* transformed with the globin DNA-containing hybrid produced β -globin-specific RNA. As compared to mature β -globin mRNA, these transcripts lacked 20–40 nucleotides from the 5' end, contained all of the small intron and extended to about the middle of the large intron. Thus, no splicing of the primary β -globin transcript could be detected in the yeast cells.

PROKARYOTIC cells are, in general, unlikely to provide an adequate environment for the spontaneous expression of chromosomal genes of higher eukaryotes. Besides the incompatibilities to be expected at the levels of RNA and protein synthesis, the existence within eukaryotic genes of intervening sequences (see ref. 1 for references), which are copied into primary transcripts and subsequently eliminated (see ref. 2 for references) by processes so far unknown in prokaryotes, suggests that only eukaryotic cells are promising hosts for testing the physiological expression of eukaryotic genes.

Yeast, as a lower eukaryote, is a possible candidate for such a test system. Vectors containing the yeast 2- μ plasmid are suitable for high frequency transformation of yeast^{3–5}, presumably because this plasmid replicates in yeast cells, yielding relatively high copy numbers and thus allowing maintenance without integration.

pJDB219, a hybrid DNA consisting of pMB9, the 2- μ yeast plasmid and the *leu-2* gene of yeast, is maintained predominantly in plasmid form in yeast⁶. We have transformed *Saccharomyces cerevisiae* with a hybrid consisting of pJDB219 and a cloned rabbit chromosomal DNA segment including a complete β -globin gene with two intervening sequences and extended flanking regions^{6,7}. We found that yeast thus transformed contained β -globin-specific transcripts 800–900 nucleotides long; however, these do not have normal termini

and have not undergone splicing. An abstract of this work has been presented⁸.

Transformation of yeast with cloned rabbit β -globin chromosomal DNA

A 5.1 kilobase-pair fragment of rabbit chromosomal DNA, containing a β -globin gene, has been cloned in plasmid pCRI (Z-pCRI/Rchr β G-1) and characterised by restriction analysis⁶; the nucleotide sequence of the gene and its flanking regions was

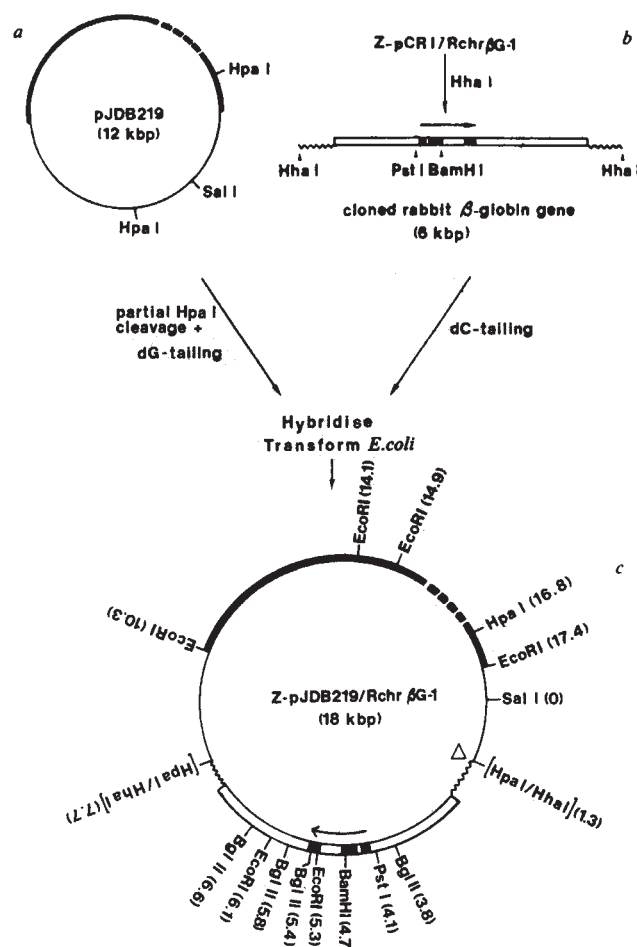


Fig. 1 Construction of hybrids consisting of rabbit chromosomal β -globin DNA, the 2- μ yeast plasmid, the yeast *leu-2* gene and plasmid pMB9. The hybrid plasmid pJDB219 (a), consisting of pMB9 (thin lines), the 2- μ yeast plasmid (thick lines) and the *leu-2* gene (dashed line) was partially digested with *Hpa*I, the fragments were separated on a 0.6% agarose gel and full-length linear DNA (12.4 kilobases) was extracted, purified on DEAE-cellulose¹⁴, digested with λ exonuclease and elongated with dGMP residues using terminal transferase²². The chromosomal β -globin plasmid Z-pCRI/Rchr β G-1 (ref. 6) was cleaved with *Hha*I, the globin-DNA-containing 6.4-kilobase fragment (b) purified by sucrose gradient centrifugation and elongated with dCMP residues²². The elongated plasmid and globin DNAs (40 ng and 10 ng, respectively) were hybridised in 50 μ l 50 mM Tris-HCl (pH 7.6), 100 mM NaCl, 5 mM EDTA for 1 h each at 65°C, 46°C and 37°C, and used to transform *E. coli* χ 1776 (ref. 6). Eight tetracycline-resistant clones were obtained and screened by the Grunstein-Hogness⁹ procedure using ³²P-labelled β -globin cDNA as probe¹⁹. Two plasmids, Z-pJDB219/Rchr β G-1 and -3 (abbreviated to YR β G-1 and YR β G-3), characterised by restriction analyses as shown in Fig. 2, were recloned in *E. coli* HB101 and used for further work. Both plasmids had the globin insert in the orientation shown (c); YR β G-3 has a 1,400 base pair deletion at the position indicated by Δ .

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determined by van Ooyen *et al.*⁷. The rabbit DNA sequence (with pCRI-derived flanking segments) (see Fig. 1) was excised with *HhaI* and elongated with dCMP residues at the 3' termini. pJDB219, which contains two *HpaI* sites, one in the 2- μ yeast plasmid region, the other within the pMB9 moiety, was partially cleaved with *HpaI*, the full-length linearised molecules were isolated, and elongated with dGMP residues (see Fig. 1). *Escherichia coli* χ 1776 was transformed with the hybridised mixture of the two DNAs, and tetracycline-resistant clones containing the globin sequence were identified by the Grunstein-Hogness⁹ procedure, using ³²P-labelled cloned β -globin cDNA as probe. Hybrid plasmids from two colonies were recloned in *E. coli* HB101, because the original clones contained a minor species of plasmid without a globin insert. Two isolates, Z-pJDB219/Rchr β G-1 and Z-pJDB219/Rchr β G-3 (abbreviated to YR β G-1 and YR β G-3), contained the β -globin *HhaI* fragment in the *HpaI* site of the pMB9 moiety in the orientation shown in Fig. 1. The two hybrid plasmids were of different size. As shown by restriction analysis (Fig. 2), YR β G-3 contained a deletion of about 1.4 kilobases at or near the junction between the plasmid and the 5' proximal part of the globin DNA insert. Both hybrids contained the

complete globin-specific DNA, as shown by the presence of the 1.7 and 0.4 kilobase *Bgl*II fragments.

S. cerevisiae MC16 leu⁻ (ref. 3) was transformed with YR β G-1 and YR β G-3 isolated from *E. coli* χ 1776 or *E. coli* HB101, and leucine-independent colonies were isolated. One yeast clone from each transformation experiment was examined in greater detail. The results described below were the same regardless of whether YR β G-1 or -3 was used, or whether the plasmid had been recloned or not. Total DNA from the transformed yeast clones, as well as the original hybrid plasmid DNAs were digested with *Pst*I and *Bgl*II, and subjected to agarose gel electrophoresis. The DNA fragments were transferred to nitrocellulose filters¹⁰ and hybridised to ³²P-labelled cloned β -globin cDNA. As shown in the autoradiogram of Fig. 3, the pattern of globin-specific bands given by the transformed yeast DNA was the same as that of the original β -globin DNA-containing plasmid Z-pCRI/Rchr β G-1. From the intensity of the bands relative to those of known amounts of β -globin DNA we estimate that there were multiple copies of globin DNA per cell. Transfer of uncleaved DNA from transformed yeast according to Southern¹⁰ followed by hybridisation with ³²P-labelled, cloned β -globin cDNA gave several bands; most preparations lacked DNA with the mobility of YR β G-1 or YR β G-3. Thus, the hybrid plasmid had been rearranged in the yeast; however, the globin-specific sequence was not changed, as shown by Fig. 3.

Characterisation of β -globin-specific transcripts in yeast

To determine whether globin-specific RNA had been synthesised in the transformed yeast cells, total RNA was subjected to agarose gel electrophoresis in denaturing conditions, transferred to diazobenzoyloxymethyl paper¹¹, and hybridised with ³²P-labelled, cloned β -globin cDNA. As shown in Fig. 4, a strong β -globin-specific band with a mobility corresponding to an RNA of 800–900 nucleotides was found in yeast cells transformed with either YR β G-1 or YR β G-3. This RNA is thus longer than mature rabbit β -globin mRNA, about 700 nucleotides¹², but shorter than the 15S β -globin precursor RNA, about 1,450 nucleotides¹³, including the poly(A) tails in both cases. By comparing the intensity of the globin-specific RNA band with that of known amounts of β -globin mRNA, we estimate that about 0.01% of the total yeast RNA was β -globin-specific.

The β -globin-specific RNA was further characterised by a modification^{14,15} of the Berk-Sharp¹⁶ hybridisation technique. To map the 5' terminus of the transcript, a 223 base-pair restriction fragment of the cloned β -globin chromosomal DNA extending from the *Mbo*II cleavage site within the first exon (position 128) to the *Pst*I site 95 nucleotides upstream from the beginning of the mRNA⁷, labelled at the 5' terminus of the minus strand (*Mbo*II cleavage site), was prepared. This probe was denatured and hybridised with the RNA sample in 80% formamide. After digestion with endonuclease S₁, the sample was denatured and the labelled DNA sized by polyacrylamide gel electrophoresis in 7 M urea. A radioactive DNA fragment is recovered if the labelled 5' terminus of the DNA probe was hybridised to the RNA; its length is a measure for the distance between the *Mbo*II site and the 5' terminus of the RNA or the beginning of extended mismatching between the RNA and the probe. As shown in Fig. 5A, natural rabbit β -globin mRNA protected a DNA fragment about 128 nucleotides in length; the DNA protected by RNA from β -globin transformed yeast cells gave five major bands, corresponding to 88, 91, 93, 102 and 110 nucleotides. The β -globin-specific transcripts from yeast apparently have several 5' termini, all of which map downstream from the position corresponding to the 5' terminus of natural β -globin mRNA. The 223-nucleotide band corresponds to the fully-protected probe and is believed to be due to self-annealing of the DNA; the presence of transcripts originating upstream, beyond the *Pst*I site, cannot be excluded.

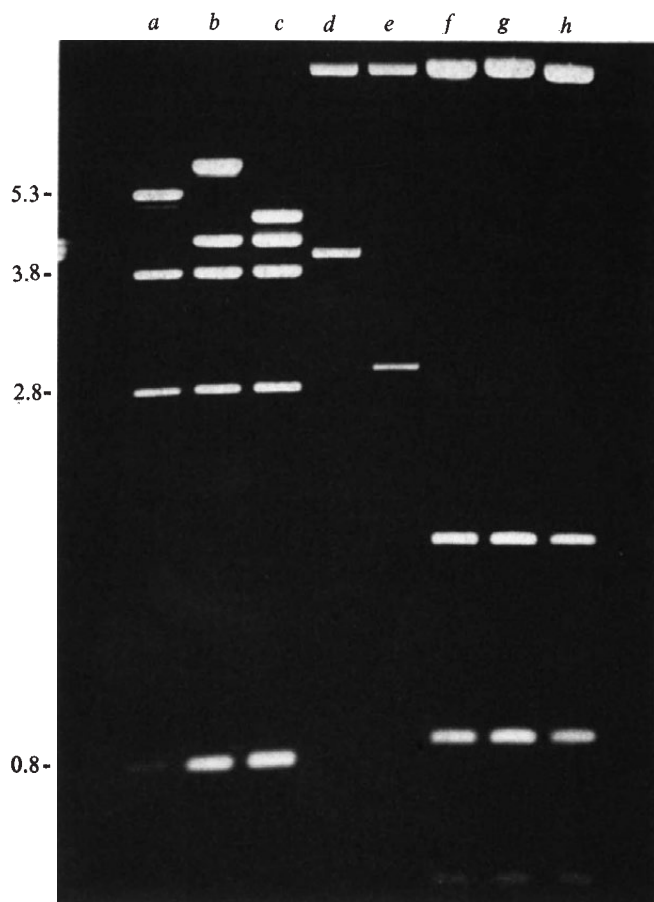


Fig. 2 Restriction site analysis of hybrid plasmids YR β G-1 and YR β G-3, containing pMB9, the 2- μ yeast plasmid, the yeast *leu-2* gene and a rabbit β -globin chromosomal DNA segment. Plasmid DNA was prepared from transformed *E. coli* HB101, by lysing bacteria with SDS²³ or Triton X-100 (ref. 24), centrifuging, and separating linear and circular DNA by the procedure of Currier and Nester²⁵, as outlined in Wilkie *et al.*²⁶. DNA was digested with the restriction enzymes indicated below and the products analysed by electrophoresis through a 1% agarose gel in 40 mM Tris, 20 mM sodium acetate, 1 mM EDTA (pH 8.2). The gels were stained with ethidium bromide and photographed in UV light. a, b and c, *Eco*RI-digested pJDB219 (ref. 3) (a), YR β G-1 (b) and YR β G-3 (c); d, YR β G-1 and e, YR β G-3, both doubly digested with *Sal*I and *Pst*I; f, g and h, *Bgl*II-digested Z-pCRI/Rchr β G-1 (f), YR β G-1 (g) and YR β G-3 (h). The orientation of the inserts was deduced from the sizes of the two largest fragments obtained by digestion with *Eco*RI (b) and (c), or *Sal*I and *Pst*I (d) and (e) (compare Fig. 1), and was confirmed by double digestion with *Eco*RI and *Pst*I or *Eco*RI and *Sal*I (not shown).

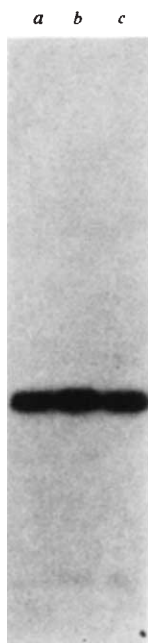


Fig. 3 Demonstration of β -globin-specific sequences in DNA from *S. cerevisiae* transformed with the β -globin DNA-containing hybrid plasmids YR β G-1 and YR β G-3. *S. cerevisiae* MC16 α leu2-3 his4-712^{ts}ade2-1lys2-1SUF2 (G. R. Fink) was converted to spheroplasts and transformed with YR β G-1 and YR β G-3 DNA as described elsewhere³. Clones of transformed yeast were selected on plates lacking leucine³. One clone from each transformation experiment (MC16/YR β G-1 and MC16/YR β G-3) was selected for further analysis. Transformed yeast was grown to late log phase in minimal medium without leucine (0.67% Difco yeast nitrogen base without amino acids, 2% glucose, 20 mg l⁻¹ adenine, lysine and histidine). The cells were converted to spheroplasts³ and DNA was isolated²⁷. DNA was digested with *Pst*I and *Bgl*II simultaneously, subjected to electrophoresis through a 1% agarose gel in 40 mM Tris, 20 mM sodium acetate, 1 mM EDTA (pH 8.2) and transferred to a Millipore membrane¹⁰. Globin DNA sequences were detected by hybridisation with the cloned rabbit β -globin cDNA fragment described earlier¹⁹, ³²P-labelled by nick-translation²⁸ (specific activity, 3.5×10^7 c.p.m. μ g⁻¹); (a) Z-pCRI/Rchr β G-1, (b) YR β G-1 and (c) YR β G-3.

To determine whether the small intron was present in the β -globin transcript, a hybridisation experiment similar to the one above was carried out, using as probe the 4 kilobase-pair *Bam*-*Sal* fragment of Z-pCRI/Rchr β G-1, labelled at the 5' (minus strand) terminus of the *Bam* cleavage site. As shown in the scheme of Fig. 6, an RNA molecule lacking the small intron would protect the probe from the 5'-³²P-labelled *Bam* site to the position where the sequences of β -globin mRNA and chromosomal DNA no longer match (at the small intron), yielding a fragment of 212 nucleotides⁷. If the small intron were present, the probe would be protected up to the region corresponding to the 5' end(s) of the transcripts, yielding fragments between 440 and 462 nucleotides. The autoradiogram of Fig. 6 shows the presence of a band at a position corresponding to about 440 nucleotides length, but no signal at the position corresponding to 212 nucleotides, proving that the small intron was present in the β -globin-specific transcripts.

Finally, the 3' termini of the transcripts were mapped using the 14 kilobase-pair *Bam*-*Sal* fragment of the β -globin chromosomal DNA plasmid Z-pCRI/Rchr β G-1 (ref. 6) labelled at the 3' (minus strand) terminus of the *Bam* site. This probe was prepared by filling up the termini of the *Bam*-cleaved β -globin chromosomal plasmid with α -³²P-deoxynucleotides using DNA polymerase I, cleaving with *Sal*I and isolating the 14 kilobase-pair fragment. Preliminary experiments showed that despite hybridisation in 80% formamide, which disfavors DNA-DNA reannealing¹⁷, a band corresponding to the full-length probe was found whether RNA was present or not. Therefore, to preclude protection of the labelled 3' terminus by

self-annealing, the *Bam* fragment was subjected to digestion with 5' λ exonuclease, sufficient to remove about 2,000 nucleotides, before cleavage with *Sal*I. Using this probe, hybridisation with RNA from yeast transformed with YR β G-1 and YR β G-3 yielded four major bands of 270, 295, 340 and 350 nucleotides (Fig. 5B). As the distance from the (filled-up) *Bam* site to the 5' border of the large intron is 18 nucleotides, the majority of the β -globin transcripts extends to about the middle of the large intron. Because, an 18-nucleotide fragment could not be detected for authentic mRNA in the conditions of this experiment, we cannot exclude the possibility that some transcripts had undergone splicing; however, because most transcripts were 800–900 nucleotides long (see Fig. 4), spliced transcripts could only constitute a minority of the population.

To determine whether the β -globin-specific transcripts were polyadenylated, yeast RNA was fractionated on oligo(dT)-cellulose, and flow-through and retained fractions were assayed for the presence of globin-specific sequences either by the transfer procedure of Alwine *et al.*¹¹ or by the modified Berk-Sharp method¹⁴. The results were variable; even with the same RNA preparation in some experiments 30%, in others 70% of

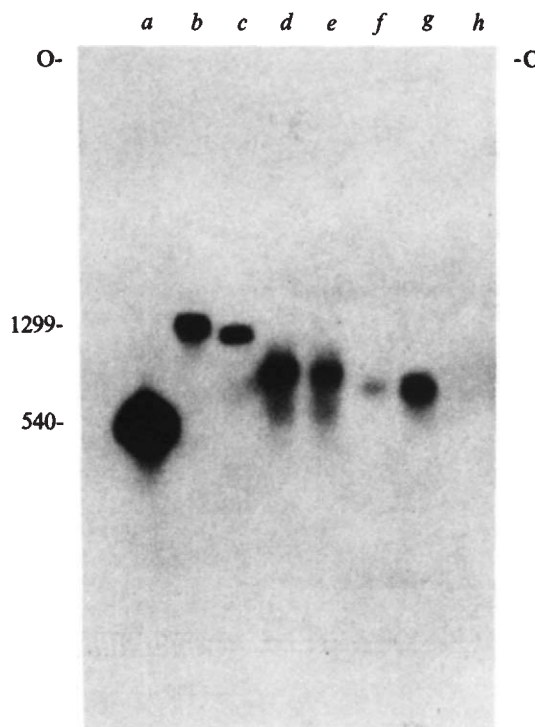


Fig. 4 The electrophoretic mobility of β -globin-specific RNA from *S. cerevisiae* transformed with the rabbit β -globin DNA-containing hybrid plasmid YR β G-1 and -3. *S. cerevisiae* was grown as described in the legend to Fig. 3. The cells were collected by centrifugation, washed in water, and suspended in 2 ml (per g of wet weight) 0.32 M sucrose, 20 mM Tris-HCl (pH 7.5), 10 mM EDTA containing heparin at 0.5 mg ml⁻¹. One volume of acid-washed glass beads was added and the sample was shaken on a vortex mixer for 1 min at top speed. The extract was diluted with 10 volumes 50 mM Tris-HCl (pH 7.5), 100 mM NaCl, 5 mM EDTA, 0.5 mg ml⁻¹ heparin, 1% SDS, extracted with phenol and chloroform, and precipitated with ethanol. 24 μ g RNA were recovered per ml culture. RNA samples were treated with glyoxal in dimethylsulphoxide at 50 °C for 60 min²⁹, subjected to electrophoresis through a 1.5% agarose gel in 10 mM sodium phosphate (pH 7), and transferred to diazobenzyloxymethyl paper¹¹. β -Globin DNA-specific sequences were visualised by hybridisation in the conditions of Alwine *et al.*¹¹ with the cloned rabbit β -globin cDNA described earlier (ref. 19 and legend to Fig. 2), ³²P-labelled to 1.6×10^8 c.p.m. μ g⁻¹ by nick translation with [α -³²P]dATP and [α -³²P]dCTP (400 Ci mmol⁻¹ each, NEN). Denatured restriction fragments of rabbit β -globin-specific DNA and rabbit β -globin mRNA were used as size markers. a, Cloned rabbit β -globin cDNA¹⁹; b and c, plasmid Z-pCRI/Rchr β G-1 digested with *Pst*I and *Bgl*II (1,299 base pairs) (b) or *Pvu*II and *Bgl*II (1,209 base pairs) (c); d and e, RNA from *S. cerevisiae* MC16 transformed with YR β G-1 (d) or YR β G-3 (e); f and g, rabbit ($\alpha + \beta$) globin mRNA 2 ng (f) or 10 ng (g); h, RNA from *S. cerevisiae* MC16 transformed with pJDB219.

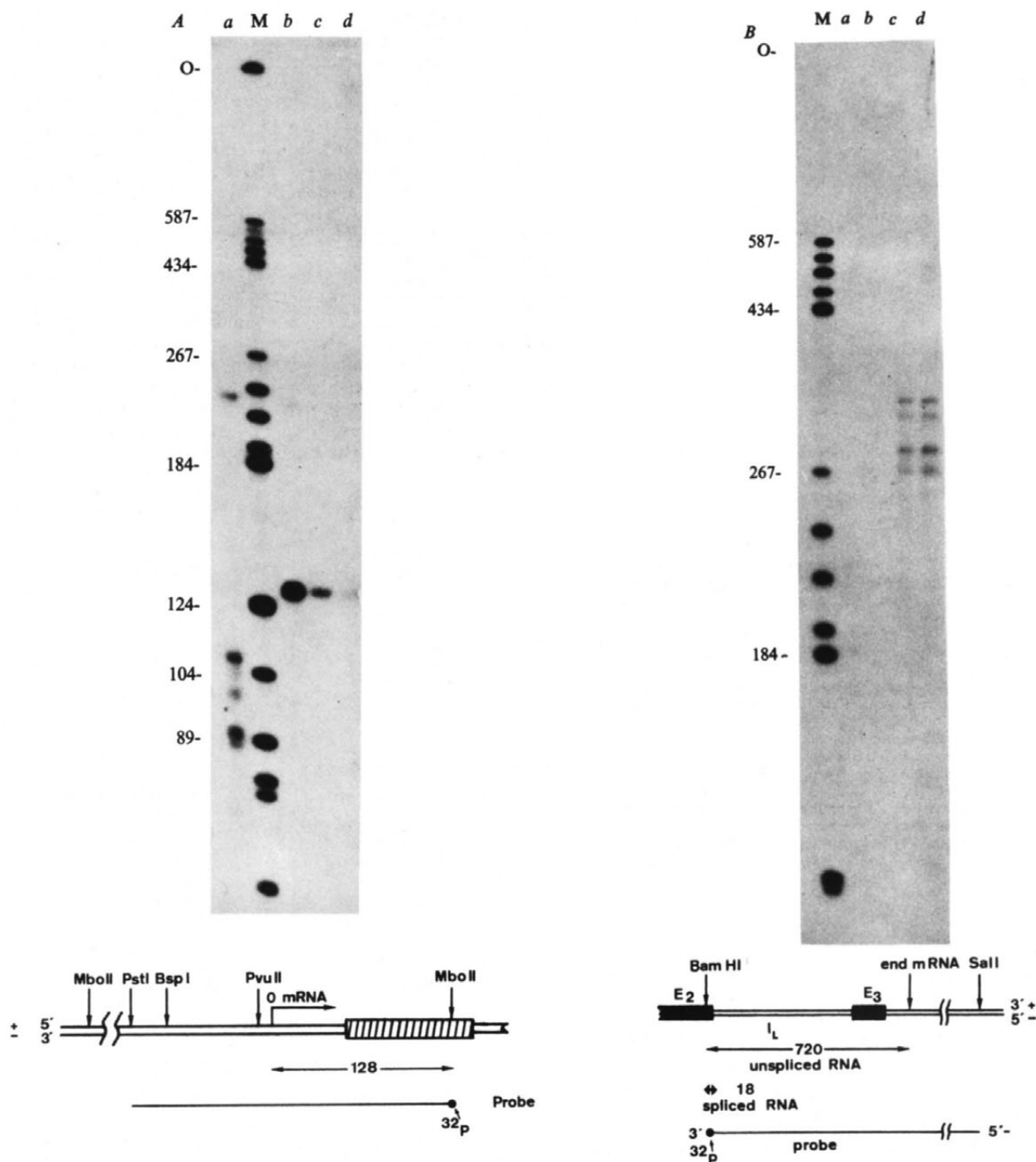


Fig. 5 Mapping of the termini of the β -globin-specific RNA from *S. cerevisiae* transformed with a rabbit β -globin DNA-containing hybrid plasmid. Mapping was carried out by a modification¹⁴ of the Berk-Sharp¹⁶ procedure. In this procedure a denatured, terminally ^{32}P -labelled DNA restriction fragment is hybridised to the RNA samples, treated with S_1 nuclease, and the length of the protected ^{32}P -labelled fragment is determined by polyacrylamide gel electrophoresis in 7 M urea. RNA from *S. cerevisiae* MC16/YR β G-1 was obtained as described in the legend to Fig. 4. **A**, Mapping of the 5' termini. The DNA probe (see bottom section of figure) was prepared as follows. Plasmid Z-pCRI/Rchr β G-1 was digested with *HhaI*, the 6.4 kilobase-pair fragment⁶ isolated by sucrose gradient centrifugation, cleaved with *MboII* and 5'-terminally labelled with [γ - ^{32}P]ATP³⁰ (specific activity, 3200 Ci mmol⁻¹). After cleavage with *PstI*, the 223 base-pair fragment was isolated by electrophoresis through and extraction¹⁴ from a 1.8% agarose gel in 89 mM Tris-borate (pH 8.2), 2.5 mM EDTA, ethidium bromide 1 $\mu\text{g ml}^{-1}$. The hybridisation reaction contained in 10 μl of 80% w/v formamide, 0.4 M NaCl, 0.04 M PIPES (pH 6.4), 1 mM EDTA, 11 ng denatured probe (about 7,000 d.p.m.) and RNA as indicated. Hybridisation was for 16 h at 57 °C under paraffin oil. The samples were digested with S_1 nuclease, extracted with phenol chloroform 1:1, and further processed as described elsewhere. Electrophoresis was in 89 mM Tris-borate (pH 8.2), 2.5 mM EDTA, 7 M urea on 5% polyacrylamide gels for 4 h at 700 V. Autoradiography was with use of Ilford fast tungstate intensifying screens, for 3 d at -70 °C. *a*, RNA (10 μg) from MC16 yeast transformed with YR β G-3; *b-d*, 3, 1 and 0.3 ng rabbit ($\alpha + \beta$)-globin mRNA; *M*, marker (pBR322 cleaved with *BspI* and 5'- ^{32}P -labelled). *O*, mRNA, position corresponding to origin of mRNA, hatched box, first segment of coding sequence. **B**, Mapping of the 3' termini. The experiment is similar to that described above, but the probe was labelled at the 3' terminus of the minus strand to permit downstream mapping (see bottom section of figure). Z-pCRI/Rchr β G-1 (4 μg), cleaved with *BamHI*, was incubated in 100 μl of 70 mM potassium phosphate buffer (pH 6.9), 100 mM NaCl, 5 mM MgCl₂, and 10 mM dithiothreitol with 3 units of DNA polymerase I (Boehringer Mannheim) and 5 μM each dTTP and dGTP, and 0.14 μM each [α - ^{32}P]dATP and [α - ^{32}P]dCTP (2 Ci mmol⁻¹, NEN) to label the 3' termini. The labelled DNA was treated with *SalI* and the larger (14 kilobase pairs) fragment, which contains the 3' proximal segment of the β -globin DNA (and the ^{32}P -labelled minus strand 3' terminus) was isolated by electrophoresis through a 0.7% agarose gel. To reduce the background resulting from self-annealing of the flush ends of the probe, the ^{32}P -labelled fragment (1 μg) was digested with 1 unit of 5' λ exonuclease^{31,32} in 50 μl of 50 mM Na-cacodylate (pH 9.5), 5 mM MgCl₂, 50 mg ml⁻¹ bovine serum albumin for 20 min at 23 °C. Each hybridisation assay (10 μl) contained 20 ng of denatured probe (20,000 c.p.m.) and RNA as indicated. The samples were processed as described above however, hybridisation was at 37 °C. Yeast RNA was prepared as described in the legend to Fig. 4. *M*, marker pBR322 cleaved with *BspI* and [^{32}P]-labelled; *a* and *b*, 4 and 1 ng ($\alpha + \beta$)-globin mRNA; *c* and *d*, RNA from *S. cerevisiae* MC16 transformed with YR β G-1 (*c*) or YR β G-3 (*d*). *E*₂ and *E*₃, second and third segments of coding sequence; *I*_L, large intervening sequence.

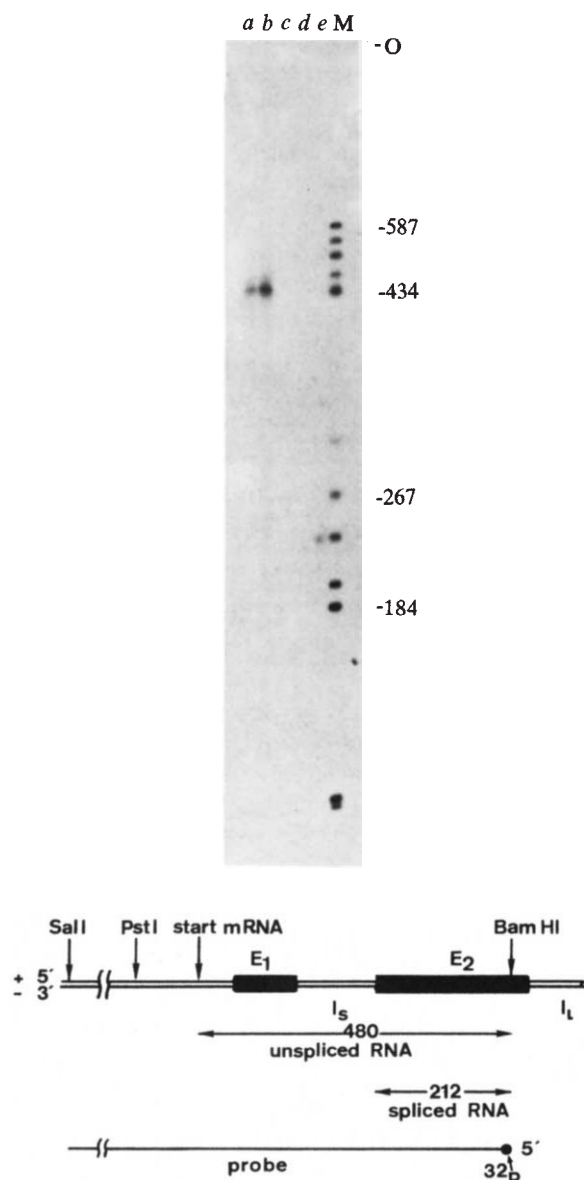


Fig. 6 Demonstration of the presence of the short intervening sequence in β -globin-specific transcripts from *S. cerevisiae* transformed with the rabbit β -globin DNA-containing hybrid plasmids YR β G-1 and YR β G-3. Mapping was carried out by the modified Berk–Sharp procedure¹⁴ as outlined in the legend to Fig. 5 and the bottom part of this figure. Yeast RNA was prepared as described in the legend to Fig. 4. The DNA probe was prepared by cleaving Z-pCRI/Rchr β G-1 with *Bam*HI, labelling the 5' termini with [γ -³²P]ATP (3200 Ci mmol⁻¹)³⁰ and cleaving with *Sal*I. The 4 kilobase-pair *Bam*-*Sal* fragment was isolated by electrophoresis through a 0.7% agarose gel. Hybridisation mixtures (10 μ l) contained 50 ng of probe (20,000 c.p.m.) and RNA as indicated. The samples were processed as described in the legend to Fig. 5 and analysed by electrophoresis through a 3.5% polyacrylamide gel in 7 M urea. M, marker (pBR322 DNA cleaved with *Bsp*I and 5' terminally ³²P-labelled); a–c, 10 μ g RNA from *S. cerevisiae* MC16 transformed with YR β G-3 (a), YR β G-1 (b) and pJDB219 (c); d and e, rabbit ($\alpha + \beta$)-globin mRNA, 1 and 4 ng, respectively. E₁ and E₂, first and second segment of coding sequence; I₁, small intervening sequence.

the globin-specific transcripts were in the retained fraction, in conditions where authentic β -globin mRNA was retained completely. This may mean that the chain length of poly(A), when present, was too short to ensure stable binding to the oligo(dT) column. A poly(A) tail of less than 15 nucleotides length appears to be insufficient to bind to oligo(dT)-cellulose¹⁸.

Discussion

RNA from yeast cells transformed with the β -globin DNA-containing hybrid plasmids was intermediate in size between mature β -globin RNA and the 15S β -globin precursor. The β -globin-specific transcripts from yeast were about 20–40

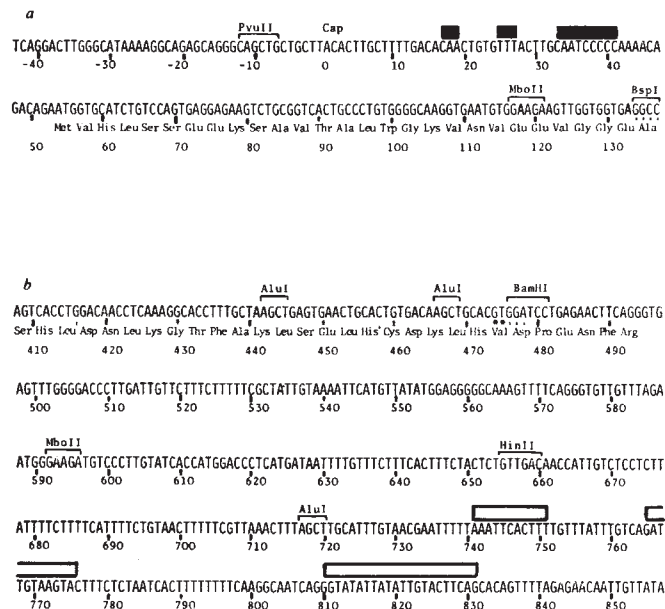


Fig. 7 Approximate map positions of the 5' and 3' termini of rabbit β -globin transcripts in yeast. The nucleotide sequence and numbering are taken from Van Ooyen *et al.*⁷. Position 1 corresponds to the capped nucleotide. The 5' and 3' termini of the β -globin transcripts map in the areas indicated by black and open boxes, respectively. a, Sequences around the beginning of the β -globin gene. b, Sequences around the 5' end of the large intron.

nucleotides shorter at the 5' end than normal globin mRNA (Fig. 7), contained the small intron and extended into the first half of the large intron where they terminated in an AT-rich region around the 250th to the 330th nucleotides of the large intron (Fig. 7), apparently heterogeneously and for the most part without a poly(A) appendage long enough to allow binding to oligo(dT)-cellulose. This should be considered in the light of the finding that the poly(A) tails of yeast mRNAs are on average considerably shorter than those of animal cell mRNAs; 50% of all yeast RNA molecules isolated on oligo(dT) cellulose have poly(A) chains less than 32 nucleotides in length¹⁸. It is not *a priori* certain that the 3' and 5' ends, as we have mapped them, correspond to the authentic termini of the transcripts. For one, the S₁ treatment may have trimmed the non-labelled end of the hybridised probe, particularly if it maps in an AT-rich region. However, S₁ digestions carried out in different conditions yielded similar patterns (R. Weaver, unpublished data) and thus do not support this hypothesis. Another possibility is that the primary transcript contained non-globin plasmid sequences at one or both ends and that a yeast-specific splicing reaction excised RNA segments comprising the junction to the globin sequence. The resulting structure would preclude detection of termini by the modified Berk–Sharp assay with a globin-specific probe. However, the length of the transcript, about 800–900 nucleotides, as estimated by its electrophoretic mobility, was in fairly good agreement with the length obtained by adding up the segments mapped upstream and downstream from the *Bam* site by the modified Berk–Sharp procedure, namely about 790 nucleotides, suggesting that no substantial segments of the transcripts escaped detection.

It is not clear whether the abnormal 5' termini of the β -globin-specific RNAs from yeast represent transcription initiation sites recognised by a yeast RNA polymerase, or whether they result from the processing or degradation of longer transcripts originating at the true promoter site or even further upstream. Similarly, the 3' termini may represent erroneous termination of transcription in T-rich regions or termini resulting from degradation or processing.

Why are the globin transcripts recovered from yeast not spliced? Possibly, yeast does not have a splicing system capable

of processing the rabbit β -globin transcript. Alternatively, the transcripts and the appropriate splicing system are not present in the same compartment. Less likely, the β -globin transcript formed in yeast may not be susceptible to splicing because it lacks part of the 5' terminal and more than a third of the 3' proximal segment; perhaps a complete transcript is required to allow the formation of a secondary or tertiary structure essential for the splicing process.

In any event, the highly heterologous system we have described is obviously inadequate for the study of transcription

and processing of the β -globin gene, which in more homologous systems, such as mouse L cells transformed with the rabbit β -globin gene¹⁹, or monkey cells infected with β -globin-SV40 hybrid DNA^{20,21} has proven capable of giving rise to normal β -globin mRNA.

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LETTERS

The composition of the Trojan asteroids

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Physical studies have shown that most asteroids are covered with material of low visual albedo ($p_v \sim 0.04$) having flat, nearly featureless reflection spectra between 0.4 and 1.1 μm (ref. 1). This large class of objects, the C asteroids, accounts for a progressively larger fraction of minor planets as one goes from the inner to the outer regions of the asteroid belt, a trend which has been interpreted as evidence of a decrease in effective condensation temperature in the original solar nebula with increasing distance from the proto-Sun². We suggest here that the very low albedos and red spectra of some Trojan asteroids can be explained by the presence of kerogen-like organic compounds. Materials containing these types of carbonaceous substances, rather than those found in the more familiar carbonaceous chondrite matrix, may have been the primary rocky condensate in the outer Solar System and may therefore be typical of the rocky component of comet nuclei.

A widely accepted interpretation of these dark, spectrally neutral materials covering the asteroids, is that they consist of silicate clay minerals (montmorillonite, chlorite, serpentine) intermixed with opaque materials such as magnetite and finely divided carbon-rich compounds. Thus, the surface materials of the C asteroids are considered to be closely similar to, and in some cases perhaps identical with, the carbonaceous chondrite meteorites. Mixtures of small amounts of magnetite and carbon black with montmorillonite can be made to match both the albedo and the general spectral reflectance of some carbonaceous chondrites, although the carbonaceous matrix material in such meteorites is much more complicated in composition than carbon black^{4,5}. The spectral reflectance curves (normalised at 0.56 μm) of the 115 km diameter C asteroid 141 Lumen, the C2 carbonaceous chondrite Murchison, and a carbonaceous construct are shown in Fig. 1.

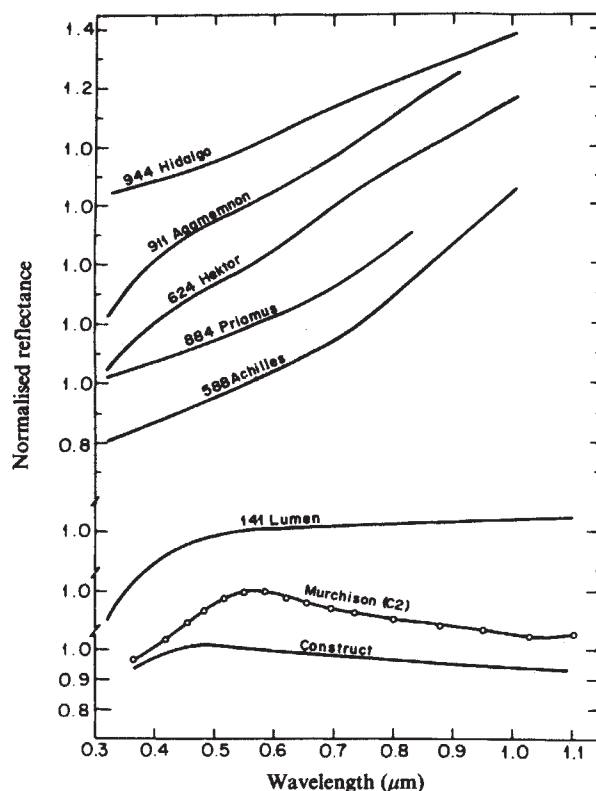


Fig. 1 Reflectance spectra of RD and C asteroids, the C2 carbonaceous chondrite Murchison, and a carbonaceous construct normalised at a wavelength of 0.56 μm . The construct is composed of 85% montmorillonite, 8% magnetite and 7% carbon (charcoal)⁵. The C asteroid is 141 Lumen. The RD asteroids are 588 Achilles, 624 Hektor ($p_v = 0.038$) and 911 Agamemnon ($p_v = 0.035$) in the preceding Trojan cloud, 994 Priamus of the following Trojan cloud and 944 Hidalgo⁷. Hidalgo is a unique asteroid in a comet-like orbit with a semimajor axis of 5.8 AU. Polarimetry and visual photometry suggest that Hidalgo may have a very low albedo⁸.

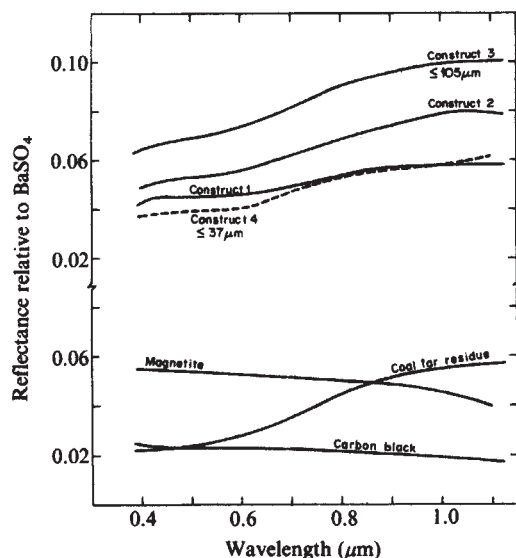


Fig. 2 The reflectances relative to BaSO₄ of several opaque substances and three carbonaceous constructs. Construct 1 is composed of 85% montmorillonite, 14.5% coal tar residue and 0.5% carbon black. Construct 2 is composed of 85% montmorillonite and 15% coal tar residue. Constructs 3 and 4 are composed of 85% montmorillonite, 7.5% magnetite and 7.5% coal tar residue. The particle size in constructs 1, 2 and 3 is $\leq 105 \mu\text{m}$ but $\leq 37 \mu\text{m}$ for construct 4.

However, there are low albedo asteroids which do not fit into the above scheme: some of the Trojan asteroids at two of the lagrangian points of Jupiter, some of the Hilda asteroids near the 2:3 commensurability with Jupiter, and the unusual asteroid 944 Hidalgo which has the second largest semi-major axis (5.8 AU) of any known minor planet. These objects have been labelled RD by Degewij and van Houten⁶ as they are very dark ($p_v \sim 0.02\text{--}0.04$) and, unlike the neutrally grey C asteroids, are spectrally reddened between 0.4 and 1.1 μm . The normalised reflection spectra of several RD objects reported by Chapman and Gaffey⁷ are shown in Fig. 1.

Degewij and van Houten⁶ have suggested two possible compositions to explain this unique combination of low albedo and red colour: (1) a material similar to the calcium-rich angrite (visual reflectance ~ 0.055); and (2) following a suggestion from Gaffey, an iron-rich clay mineral similar to the matrix material of C1 and C2 carbonaceous chondrites but without the usual attendant opaque phases (magnetite and carbon-rich compounds). Both suggestions have difficulties. In the first, the connection with the angrite seems implausible as the single known angrite is classified with the eucrites as basaltic achondrites⁸, which are the products of high-temperature processes that are unlikely to have occurred commonly in small bodies in the outer system. It is also difficult to resolve the absence in the RD spectra of the band near 1 μm prominent in the angrite spectrum. The second suggestion is simply incompatible with the extremely low visual geometric albedo of RD objects.

We propose that the nature of the RD objects can be explained better by the presence of very opaque, very red, polymer-type organic compounds, which are structurally similar to aromatic-type kerogen. Kerogen-like substances compose the bulk of the organic material in some carbonaceous chondrites⁹. These compounds probably result from non-biological processes in the early solar nebula—for example, materials from Fischer-Tropsch-type reactions between carbon monoxide and hydrogen at a few hundred degrees kelvin with iron metal, magnetite or silicate clay dust as possible catalysts may have been thermally altered to produce aromatic rich opaques⁹⁻¹².

Kerogen substances can be obtained by removing all solubles from ordinary coal tar. The spectral characteristics of the solubles have been investigated elsewhere¹³. The spectrum of the kerogen-like carbonaceous non-soluble residue left after dissolving coal tar in solutions of hexane, toluene and acetone measured with the Cornell goniometer is compared with those of carbon black and magnetite in Fig. 2. Of importance is the extremely low reflectance (0.02) of the coal tar residue in the visible compared to magnetite, and the strong increase in reflectance at the longer wavelengths compared with carbon black. Also shown in Fig. 2 are the spectra of various combinations of powdered montmorillonite, magnetite, the non-soluble residue from coal tar, and carbon black. Constructs 1, 2 and 3 are composed of grains $\leq 105 \mu\text{m}$. Construct 4 is the same composition as construct 3 but composed of grains $\leq 37 \mu\text{m}$. The decrease in reflectance with decreased grain size is opposite that observed for the clay minerals montmorillonite and chlorite¹⁴ but can be explained by the extremely efficient coating ability of finely divided, opaque coal tar residue in a manner similar to that caused by submicrometer particles of lampblack. The normalised spectral reflectance curve of constructs 3 and 4 are compared with the normalised spectra of two RD asteroids in Fig. 3.

All constructs provide good matches to the observed photometric properties of the RD objects: low albedos and very red spectral reflectance curves. It is not necessary to postulate analogues of basaltic achondrites or opaque-poor clays. Mixtures of clays, magnetite, carbon black and an opaque, carbon-rich substance similar to terrestrial kerogen match the observed

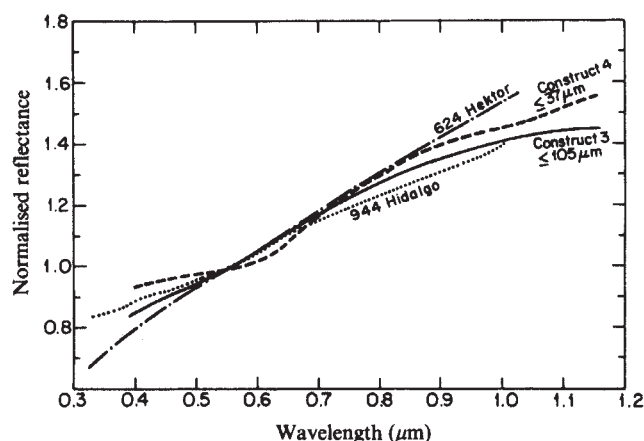


Fig. 3 The normalised reflectance of constructs 3 and 4 compared with two RD asteroids: 944 Hidalgo and 624 Hektor.

properties of RD asteroids and are cosmochemically likely to have been produced in the outer Solar System.

Our essential ingredient—the non-soluble residue—may have required lower temperatures for its formation and preservation than the carbonaceous materials in the carbonaceous chondrites and C asteroids. It is significant that a carbon-rich extract from the C3V meteorite Allende measured by Johnson and Fanale⁴ has a spectrum unlike that of the non-soluble residue, but similar to that of carbon black, that is, the reflectance increases towards the shorter wavelengths and falls towards the IR. We suspect that the carbonaceous residue from Allende is not representative of the more primitive and unaltered carbon-rich material found in RD objects. This suggestion would explain why RD objects have not been detected closer than ~ 4 AU from the Sun, and implies that beyond the orbit of Jupiter RD material might replace C asteroid material as the typical condensate. If this suggestion is valid, the rocky material in comets should resemble RD material more closely than that found in the C asteroids.

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IR brightness and eclipse cooling of Saturn's rings

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Equatorial scans of Saturn at 20 μm wavelength, obtained with the Mayall 4-m telescope in 1978–79, show a continuing decrease in the specific brightness of the A and B rings as the ring plane projection approaches an edge-on apparition. The decreased brightness of the previously dominant B ring reveals more clearly a large ($\sim 30\%$) difference in brightness between the east and west ansa portions of the C ring, in contrast to a barely discernible difference for the other ring ansae. The amount of eclipse cooling is compatible with a C ring particle size of ~ 1 cm. We propose here that the B ring brightness variation could partially result from a decrease of absorbed insolation by a modest amount of visible scattering.

Over the past few years we have monitored the 20 μm IR brightness of Saturn's rings with respect to the changing inclination of the ring plane toward the Sun (B'). During this time a large change in ring tilt has occurred. The ring plane attained its maximum tilt of about 26° in 1973 and will be edge-on in early 1980. On four occasions since March 1977 we have measured the ring brightness temperatures with the Kitt Peak National Observatory (KPNO) 4-m Mayall telescope and closed-cycle-cooler photometer system. The nominal 1 mm cold aperture in the focal plane produces a typical beamwidth (FWHM) of 2 arc s.

Figure 1 shows the equatorial scan obtained in January 1979 for a solar elevation angle relative to the ring plane (B') of -6.5° . A computer model fit to the scan is also shown. The model assumes a uniform brightness for each ring component and is more fully described elsewhere¹. We have normalised the ring brightnesses relative to a disk centre temperature of 89.4 ± 2 K, which assumes that the temperature has decreased by 0.5 K since our first March 1977 observation due to the 2% increase in Saturn's heliocentric distance. This correction assumes equal solar and internal heat sources^{1–3}.

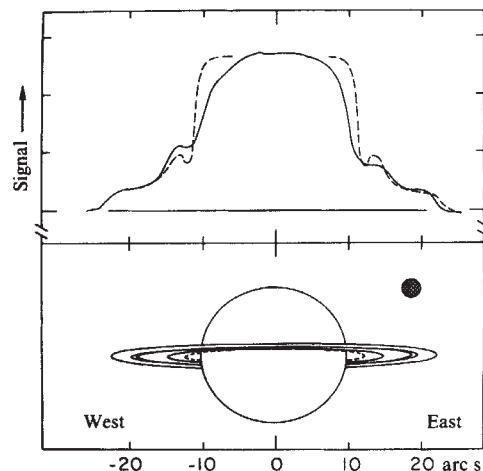


Fig. 1 Equatorial scan of Saturn at 19.7 μm and $B' = -6.5^\circ$ obtained on 10–11 January 1979. The diameter (FWHM) of the telescope point source response function is shown by the cross-hatched circle. The dashed line shows the result of a two-dimensional convolution of the telescope function and the Saturn geometry which defines the ring brightness temperatures. In this calculation a uniform brightness temperature is assumed for each ring component so that the discrepancy between the model result (---) and the experimental scan (—) at the C-ring ansae shows the difference attributed to eclipse cooling.

Comparing these results with our 1978 measurements confirms the pronounced difference in brightness between the east and west ansa positions of the C ring. The fact that a similar difference in brightness was evident in these data (see Fig. 1, ref. 4), when the larger ring inclination of $\sim 12^\circ$ excluded most of the B ring contribution to the beam at the C ring ansae positions, leads us to associate the observed brightness difference with the C ring. The brightness temperature for the east C ring ansa position is 81.5 K and for the west ansa 85 K, based on the above disk centre temperature of 89.4 K. The post-eclipse east ansa segment is 0.7 as bright as the corresponding west ansa segment.

Aumann and Kieffer⁵ calculated particle size versus eclipse heating and cooling for possible ring materials. The observed amount of eclipse cooling, taking into account the $\sim 2,000$ s from eclipse exit to the east ansa orbit position, suggests a mean particle size of the order of 1 cm. The A and B rings do not show a significant brightness difference between the east and west ansa segments. Even allowing for the longer orbital periods in this case, the evidently much smaller eclipse cooling at the ansae would seem to exclude the same size composition for these rings. The C ring continues to show no decrease in brightness with respect to changing solar elevation, in contrast to the A and B rings¹.

Table 1 summarises the average ansa brightness temperature of the B ring over the observable range of ring inclination. In Fig. 2 these results are compared with three different ring models with respect to the B' dependence. While the multiple scattering model of Kawata and Irvine⁶ is notable for its excellent match to

Table 1 20- μm brightness temperatures for the B-ring adjusted to a common heliocentric distance of 9 AU

Saturnicentric solar latitude $ B' $	B-ring brightness temperature (K)	Year of observation	Refs
24.8°	90.0 ± 3	1971	8
26°	93.8 ± 2	1972–73	9–11
16.3°	84.3 ± 2	1977	1
11.8°	77.5 ± 3	1978	This work
6.5°	74.0 ± 3	1979	This work

visible observations, this model is incompatible with the observed B' dependence of the B-ring brightness at $20\text{ }\mu\text{m}$.

The discovery of dark carbonaceous ring systems around Uranus and Jupiter led us to attempt to fit the B-ring brightness temperature with a simple two-component model consisting of dark particles sandwiched within a haze of small, icy particles. In this model the C ring is composed of dark particles alone, the less dense ice particles having been swept away by the Poynting–Robertson effect. Significant scattering of the visible solar insolation in the A and B ring occurs in the overlying layers of bright icy particles while the principal absorption and IR emission occurs in the embedded dark material. The dark material comes into thermal equilibrium with solar and planetary radiation components. The IR radiation in the direction of the Earth from the ring has three components: (1) the attenuated direct rays from the embedded dark particles; (2) the radiation scattered in the Earth direction by all points of the upper bright particle layer; and (3) the re-emission of radiation absorbed by the bright upper layer (the absorption of solar radiation by the bright layer is considered negligible).

In the calculation illustrated in Fig. 2, the solar constant is 17.2 W m^{-2} at 9 AU. A good fit is obtained for a total optical depth of 1 in the visible with the embedded dark layer having an optical depth of 0.90 and the bright particle layers over and underlying the dark particles an optical depth of 0.05 each. At $20\text{ }\mu\text{m}$ we assumed the same optical thickness for each layer as in the visible, and a single scattering particle albedo of 0.2 for the ice type particles. Finally, we assumed a constant thermal flux from Saturn of 3 W m^{-2} which accounts for the edge-on temperature limit of 70 K for zero inclination. The essential feature of this model is the scattering of visible solar insolation by a small particle fraction ($\sim 10\%$) of the total optical depth. The remaining specifications for a complete model would, of course, have to consider the optical and radar properties.

The experimental data can be equally well described by a $\sin^{1/4}|B'|$ dependence plus a constant planetary heating term equal to about 60 K. This is equivalent to an idealised Lambert surface which may represent the behaviour of a multi-layer particle model with certain simplifying assumptions according to Pollack⁷. Our most recent point for $\sin|B'| \approx 0.1$ suggests a possible inflection in the curve such as is seen in the two-component model result. Observationally it should be possible to obtain measureable ring signals for $\sin|B'|$ as small as 0.05. Such a measurement should be attempted in the latter part of 1980.

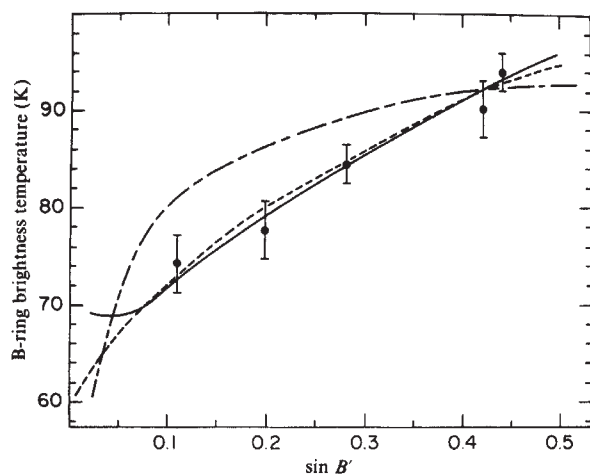


Fig. 2 The B ring brightness temperatures versus the sine of the solar elevation angle. The experimental data are given in Table 1. The three models compared here are: (1) —, a two-component model discussed in the text; (2) ---, a $\sin^{1/4}|B'|$ plus constant dependence equivalent to Lambert type behaviour; and (3) - · - ·, the results computed by Kawata and Irvine for a multiple-scattering model (their Model B).

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The photoelectrochemical effect at a p-GaP electrode

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Increasing attention is being focused on the properties and behaviour of p-type semiconductor electrodes. For instance, p-type GaP electrodes have been used in photoelectrochemical cells for water splitting¹, CO₂ reduction² and N₂ fixation³. We report here the quantum efficiency–potential characteristics for H₂ evolution at an irradiated p-GaP electrode. The curves have been evaluated using a Schottky barrier model of the semiconductor/electrolyte interface⁴.

The H₂ evolution reaction at a p-type semiconductor electrode involves the transfer of photogenerated electrons from the conduction band edge (and via surface states) to H₃O⁺ acceptor levels. For wide band gap non-corroding p-type semiconductors the H₂ evolution reaction is driven, in certain conditions, by a built-in overpotential (U_c) given by:

$$U_c = E_g - 1.23 - V_{sc}^{s-c} - \Delta E_F \quad (1)$$

where E_g is the energy gap, V_{sc}^{s-c} is the potential drop across the space charge layer when the p-type semiconductor cathode is short-circuited to the anode and ΔE_F is the difference between the Fermi level and the valence band. An energy diagram of a p-type semiconductor/electrolyte/metal cell is shown in Fig. 1.

Solid state kinetics is favoured over electrochemical kinetics when U_c is large, which is frequently the case for wide band gap semiconductors. For p-GaP it was estimated that $U_c \sim 1.2\text{ V}$. Therefore, for conditions which include low light intensities, sufficient cathodic bias and concentrated electrolyte it is appropriate to apply Schottky barrier theory to describe the quantum efficiency of H₂ evolution from a p-GaP electrode as a function of potential. According to this theory the quantum efficiency (η) is given by⁴:

$$\eta = 1 - \frac{\exp[-\alpha(\lambda)W_0\Delta V_{sc}^i]}{1 + \alpha(\lambda)L_n} \quad (2)$$

where $\alpha(\lambda)$ is the absorption coefficient at a specified wavelength λ , W_0 is the space charge width for 1 V across the depletion layer, L_n is the electron diffusion length and ΔV_{sc} is the potential drop across the semiconductor space charge layer. The parameter ΔV_{sc} is the difference between the potential at the semiconductor surface and the flat band potential. The

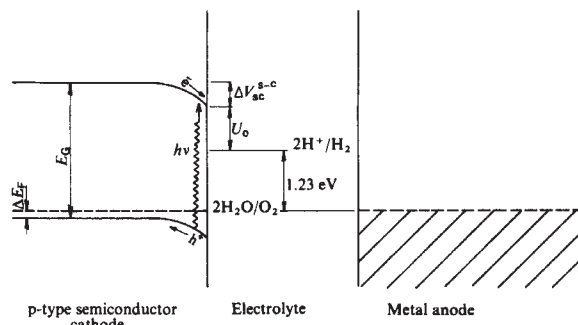


Fig. 1 Energy level diagram of a p-type semiconductor/electrolyte/metal system.

difference is proportional to the applied potential. For equilibrium short-circuit conditions ΔV_{sc} equals ΔV_{sc}^{s-c} in the absence of surface states.

An ohmic contact to a single crystal of p-type GaP (Zn doped; 111 face; $N_A \sim 2 \times 10^{16} \text{ cm}^{-3}$; $\rho \sim 2 \Omega \text{ cm}$) was formed by soldering an In–Zn alloy onto the back of the sample. The crystal was then fabricated into an electrode by positioning it in a Teflon holder and fixing it with epoxy resin. Before the experiment the p-GaP electrode was etched in a $\text{HNO}_3:\text{HCl}$ (2:1) mixture for 2 min.

The cell p-GaP/1M NaOH/Pt was studied. Nitrogen was bubbled through the electrolyte for 20 min before the experiment. Monochromatic irradiation was obtained by passing polychromatic light from a 900 W xenon source through a high intensity Bausch and Lomb monochromator. Photocurrent–voltage curves were measured and recorded (potentiostatically) in the usual manner whilst irradiating the p-GaP electrode with light of wavelengths 4,400, 4,500 and 4,600 Å. Irradiation intensities were measured with a Zeiss thermopile model VT Q3/A. The quantum efficiency–voltage relationships were determined from the photocurrent–voltage curves using the expression:

$$\eta = \frac{i_{ph} - i_{dark}}{N_{ph}(O)} = \frac{\text{No. of photoelectrons}}{\text{No. of incident photons}} \quad (3)$$

where i_{ph} and i_{dark} are the electrode current densities with and without illumination respectively.

Quantum efficiency–potential curves were calculated from the photocurrent–voltage curves at three different wavelengths ($\lambda = 4,600, 4,500$ and $4,400$ Å). The $\alpha(\lambda)$ s for GaP at these wavelengths were $< 5 \times 10^4 \text{ cm}^{-1}$. If $\alpha(\lambda) \geq 10^5 \text{ cm}^{-1}$ surface recombination effects which become significant due to the high

Table 1 Parameters calculated from the quantum efficiency–voltage curve fitting analysis for irradiated p-GaP in 1M NaOH

Wave-length (Å)	(Photocurrent) ² –flat band potential (V versus SCE)	$\alpha(\lambda)W_0$	Mean deviation (%)	$\alpha(\lambda)L_n$	Mean deviation (%)
4,400	–0.64	0.92	2.0	2.2×10^{-3}	1.8×10^3
4,500	–0.64	0.64	2.8	9.8×10^{-4}	1.0×10^3
4,600	–0.64	0.27	3.8	3.4×10^{-4}	1.0×10^3

Table 2 Comparison of the $\alpha(\lambda)W_0$ terms from curve fitting with $\alpha(\lambda)W_0$ terms calculated using $\alpha(\lambda)$ s from ref. 6

Wavelength (Å)	$\alpha(\lambda)$ (cm^{-1}) (from ref. 6)	$\alpha(\lambda)W_0^*$ (using $\alpha(\lambda)$ from ref. 6)	$\alpha(\lambda)W_0$ (curve fitted values)
4,400	2.24×10^4	0.55	0.92
4,500	1.57×10^4	0.39	0.64
4,600	6.16×10^3	0.15	0.27

* W_0 was calculated as $2.47 \times 10^{-5} \text{ cm V}^{-1}$ from equation (4) using $\epsilon = 11$ (ref. 7).

Table 3 Comparison of the calculated and experimental ratios⁶ of the absorption coefficients for p-GaP in 1M NaOH

Ratios	Experimental (from ref. 6)	Curve fitting
$\alpha(4,400 \text{ Å})W_0/\alpha(4,500 \text{ Å})W_0$	1.4	1.4
$\alpha(4,500 \text{ Å})W_0/\alpha(4,600 \text{ Å})W_0$	2.5	2.4
$\alpha(4,400 \text{ Å})W_0/\alpha(4,600 \text{ Å})W_0$	3.6	3.4

concentration of hole–electron pairs created close to the surface have to be taken into account in the expression for η .

A nonlinear least-squares computer program was used to fit equation (2) to the experimental quantum efficiency–voltage curves. Two adjustable parameters, $\alpha(\lambda)W_0$ and $\alpha(\lambda)L_n$, and the flat band potentials determined from (photocurrent)²–potential plots were used. Table 1 lists the flat band potentials and also the values determined for $\alpha(\lambda)W_0$ and $\alpha(\lambda)L_n$, from the least squares analysis of each curve together with the respective mean deviations of the latter parameters.

The experimental and theoretical quantum efficiency–voltage curves are shown in Fig. 2. The mean deviations of the $\alpha(\lambda)W_0$ terms were small ($< 4\%$) whilst those of the $\alpha(\lambda)L_n$ terms were

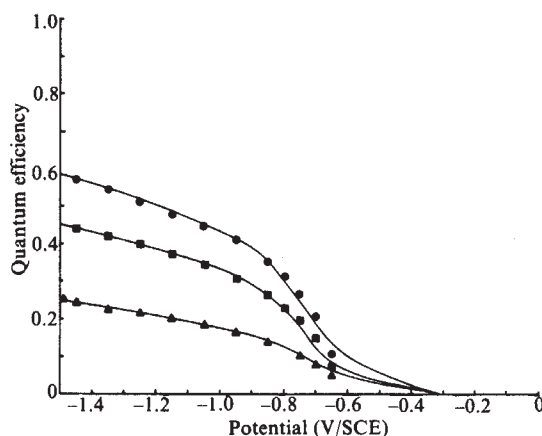


Fig. 2 Experimental (solid lines) and calculated (points) quantum efficiency versus voltage curves for p-GaP in 1M NaOH illuminated by 4,400 (●), 4,500 (■) and 4,600 (▲) Å light.

large ($\sim 1,000\%$). The large uncertainties in the $\alpha(\lambda)L_n$ terms are due to the fact that their magnitudes are small in comparison to 1.0 which in turn means that their values cannot be determined accurately via a nonlinear least-squares fit of equation (2). Physically, the latter result implies that the contribution of electrons, photogenerated in the bulk region of the semiconductor, to η , is small.

The parameter W_0 is defined by⁴:

$$W_0 = \left(\frac{2\epsilon\epsilon_0}{e_0 N_A} \right)^{1/2} \quad (4)$$

where ϵ_0 is the permittivity of a vacuum, e_0 is the electronic charge, ϵ is the semiconductor dielectric constant and N_A is the acceptor density. Table 2 lists the $\alpha(\lambda)W_0$ values obtained from the computer fitting with the $\alpha(\lambda)W_0$ values calculated using the $\alpha(\lambda)$ s that have been reported previously for the respective wavelengths⁶ and W_0 calculated from equation (4). The agreement between the $\alpha(\lambda)W_0$ terms calculated by the two different methods for each wavelength is satisfactory (within a factor of two) considering the uncertainty in the value of N_A .

A quantitative analysis of the $\alpha(\lambda)W_0$ terms (determined from the least squares fitting) consisted of comparing their ratios with the ratios of the p-GaP absorption coefficients for the respective wavelengths that have been reported previously⁶.

The literature and computer fitted ratios are compared in Table 3 and the agreement is close (within 6%). Hence for the first time a quantitative correlation has been observed between the experimental quantum efficiency-potential curves for a p-GaP electrode and the respective fitted curves derived from a Schottky model of the semiconductor/electrolyte interface.

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Analogous Upper Proterozoic apparent polar wander loops

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The ~1,100 Myr Grenville mobile belt of the Laurentian (North American) Shield yields a record of uplift magnetisations defining a closed apparent polar wander (APW) loop¹⁻⁴ nearly identical to the contemporaneous palaeomagnetic records from the Sveconorwegian belt of the Fennoscandian Shield and ~1,100–800 Myr supracrustal successions of the African Shield. The palaeomagnetic data reported here show that these Shields were contiguous at this time⁴, and comparison with the pre-1,100 Myr palaeomagnetic record defines a relative rotation of the Fennoscandian Shield with respect to the other major shields at ~1,100 Myr, although they remained in close proximity until late Precambrian times. Tectonic and palaeomagnetic correlations between the major shields suggest that this motion represented an early fragmentation of rigid sialic crust. The restriction of crustal mobility to long linear mobile belts and the progressive contraction of anorogenic magmatism both define a gradual consolidation of the Proterozoic crust as temperature gradients declined.

Considerable attention has recently been devoted to determining the tectonic significance of palaeopoles from the Grenville Province¹⁻⁴; a concerted evaluation has involved reconsideration of the Grenville palaeopoles in the context of the uplift and cooling history of this plutonic terrain^{3,5}, attempts to define the APW path from the remainder of the Shield during this interval^{4,6}, and isotopic studies using ⁴⁰Ar/³⁹Ar step heating determinations and diffusion characteristics to calculate both an age and synchronous temperature for minerals from the belt⁷. A relative chronology of the Grenville poles has been established using thermochron zones, which assumes that cooling and magnetisation of the belt followed the scheme defined by K–Ar mica ages; the mean poles defined by selected age intervals are illustrated in Fig. 1a (after ref. 2). They define the motion of APW as a closed loop although the age limits of the zones are regarded only as a first approximation to the ages of magnetisation^{3,7}. Two more direct estimates by Berger *et al.*⁷ use thermochronometry to estimate the ages of TRM components in the Haliburton intrusion (Hb₁ and Hb₃ in Fig. 1a) at ~980 and 820 Myr respectively.

The latest assessments agree that the Grenville loop represents an integral part of the total Laurentian APW path^{3,4,7} and defines a post-1,030 Myr sequence which fits the sporadic coverage of the same interval from the remainder of the Shield^{3,4}. Following refs 2 and 6 the earliest part of the Grenville

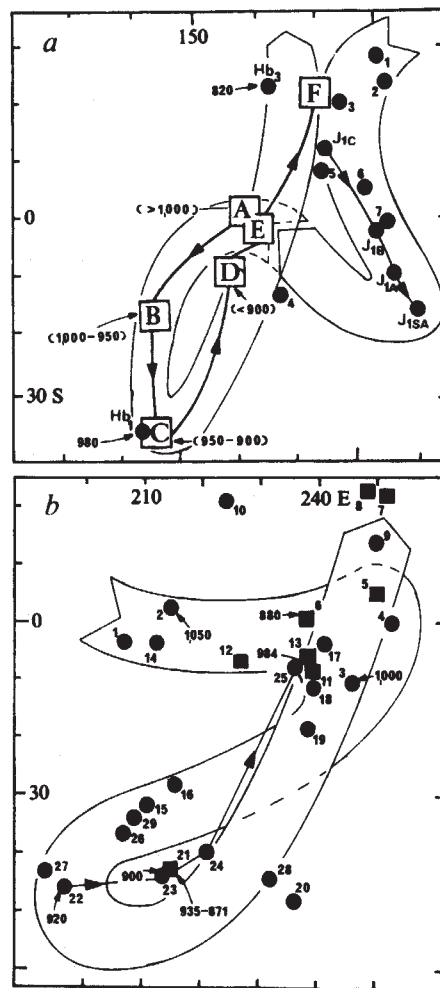


Fig. 1 Laurentian palaeomagnetic poles for the interval ~1,100–800 Myr. Numbered poles with ages in brackets are 1, Mamainse lavas, normal (1,070); 2, Portage Lake lavas (1,100); 3, Copper Harbour lavas (1,080); 4, Nankowap Formation (1,000); 5, Freda and Nonsuch Sandstone (1,040); 6, Pikes Peak granite (1,030); 7, Cardenas lavas (1,090). J1C to J1SA are the sequence of poles defined from the Jakobsville Formation⁶. The palaeomagnetic data from the Grenville Province are illustrated as mean poles A to F from thermochron zones and age assignments are a first order approximation only²; specific magnetisations Hb₁ and Hb₃ are dated by isotopic studies⁷. b, Fennoscandian 1,050–800 Myr palaeomagnetic poles (summarised in refs 9 and 10) derived from Sveconorwegian uplift magnetisations (●) and igneous intrusions into pre-Sveconorwegian terrain (■). Poles with age assignments in brackets are: 1, Bamble and Köngsberg metamorphic rocks (1,100–950 Myr); 2, Kragerö intrusions (1,050 Myr); 3, 4, Älgön, Brattön norites; 5–10, Väby, Tärno (880 Myr), Bräkne-Hoby (975–880 Myr) Fåjö, Listed and Bolshavn dykes; 11, Nistrop sill (984 Myr); 12, Årby dyke (995 Myr); 13, Falun dyke (966–914 Myr); 14–18, intrusions in Sveconorwegian margin ('Schistosity' zone); 19, Tuve dyke; 20, SW Sweden amphibolites; 21, Karlshamn dyke (935–871 Myr); 22, Aana-Sira amphibolites; 23, 24, 25, Rogaland igneous complex A, B, C; 26, Egersund anorthosite; 27, 28 SW Norway farsundite; 29, Hunnedalen dykes (900 Myr).

loop in Fig. 1a is connected to a swathe defined by other poles dated 1,100–1,030 Myr. In addition, careful demagnetisation studies⁶ have identified a time sequence of palaeopoles from the Jakobsville Formation (J1C–J1SA in Fig. 1a) which the authors suggest defines APW motion over the time interval 1,070–1,040 Myr. The youngest part of the Grenville loop also correlates with a range of palaeopoles from elsewhere in the Shield^{3,6} although ages of magnetisation are poorly defined. Because most of the poles from the Grenville Province are

derived from multicomponent magnetisations, uncertainties must surround both their precise position and their age²; also the link between the Jakobsville and Grenville poles is not, as yet, completely clear⁶. For these reasons it is not certain that the Grenville loop is anticlockwise (see refs 1, 4, 6, 7) as defined by the thermochron zones², and it is possible that polar trends over shorter periods were more complex. However, it is clear that the outward and return paths of the loop were very close together, and bearing in mind uncertainties in individual poles of 5–10° and a conventional APW swathe width of 15–20°, these points are not critical to the analysis that follows although they do impose limitations on the definition of the geological model.

The Sveconorwegian mobile belt of southern Norway and south-west Sweden⁸ is a zone of medium-high grade plutonic rocks deformed at 1,100–1,000 Myr, and uplifted and cooled over a long interval after this. The palaeomagnetic data from this belt are shown in Fig. 1b. Insufficient K–Ar mineral ages are available to attempt a thermochron analysis^{3,5} of these data, but we have the advantage of a contemporaneous body of data from dolerites intruded into cold crust of the adjacent (Svecofennian) zone and linked to Rb–Sr determinations⁹. Agreement with

uplift magnetisations of the Sveconorwegian belt is close (Fig. 1b). The oldest part of the loop is defined by basement rocks of the Bamble and Kongsberg regions¹⁰ with magnetisations linked to Rb–Sr and K–Ar studies¹¹ indicating an age of 1,050 Myr, and the base of the loop is linked to age dates in the range 935–900 Myr. The return path is defined in part by magnetisations of the Rogaland igneous complex^{10,12,13} of which the latest phase is dated 842 Myr (ref. 14) and pole 25 is inferred to be somewhat younger than this¹⁰.

The contemporaneous APW path for Africa is currently less well defined, but is of comparative interest because the data are derived from supracrustal sedimentary/volcanic suites. A loop here is defined by a stratigraphically controlled sequence of poles from the 1,000–800 Myr Bukoban System of Tanzania (ref. 15, Fig. 2a) and limited data from southwestern Africa^{5,15}.

We observe that the 1,050–800 Myr palaeopoles from each of these Precambrian Shields define a flattened APW loop of comparable chronology, size and shape (Fig. 2b). The similarity is so close that identical polar movement seems to be recorded relative to each shield; critical points in the correlation are the 1,000–900 Myr and 900–800 Myr links of the Laurentian and Fennoscandian paths and the 1,100–1,040–1,000 Myr arms of the African and Laurentian paths. The principal remaining problem with direct correlation is the distribution of age estimates for the base of the loop ranging from a maximum of 980 Myr from the high blocking temperature component of the Haliburton intrusion⁷ to a minimum of 820 Myr for the Gagwe lavas¹⁵; the latter is a K–Ar determination on lavas exhibiting advanced stages of hydrothermal alteration and is likely to be on the low side.

The tectonic significance of these loops is that when superimposed they yield a reconstruction with the Shields in direct continuity (Fig. 3b). The existence of the African–Laurentian link before 1,100 Myr is supported by a range of palaeomagnetic and tectonic evidence¹⁶, and although this link has been disputed¹⁷, I have argued elsewhere that the case rests on an oversimplification of the palaeomagnetic record for the Laurentian Shield¹⁸. The Laurentian–Fennoscandian configuration however, cannot be reconciled with the pre-1,200 Myr data^{16,19,20} which support a contiguous configuration but with the Sveconorwegian and Grenville belts in close alignment (Fig. 3a)²⁰. This relative motion of the Fennoscandian and African–Laurentian Shields is further indicated by the convergence of their separate APW paths in the correlation of Fig. 2b, and the net motion is a clockwise rotation (~110°) of the Fennoscandian Shield about a local axis of rotation in the Baltic Sea.

Whether or not this net rotation was the only motion involved cannot be decided at present because of the paucity of Fennoscandian data relating to the interval of motion (~1,200–1,000 Myr). However, it seems likely that rupture and reimpingement of the two Shields involved some strike-slip motions because there is consistent evidence for dextral motion along the Grenville Front between 1,200 and 1,000 Myr in the form of deformation and displacement of the Labrador Trough² and opening of the Keweenaw rift system^{21,22}. Impingement of the two shields in a new configuration could account for this large regional stress system, and it also produced crustal thickening of the mobilised continental margins represented by the Grenville and Sveconorwegian belts^{2,23}. Direct consequences of this thickening were the extensive intrusion of large anorthosite, gabbro, and related plutons and the protracted crustal uplift²⁴; the Grenville Front and 'Schistosity Zone' (the latter separating the Sveconorwegian belt from the previously-stabilised sector of the Fennoscandian Shield) define the abrupt limits of this remobilised terrain. Note also in Fig. 2b that there is slight mismatch between the pre- and post-1,000 Myr segments of the African and Laurentian APW curves; this might simply reflect the poor control of the African curve, but may also be interpreted in the context of relative (sinistral) motion between the two Shields at about this time.

Does this fracturing and rotation of the Fennoscandian Shield

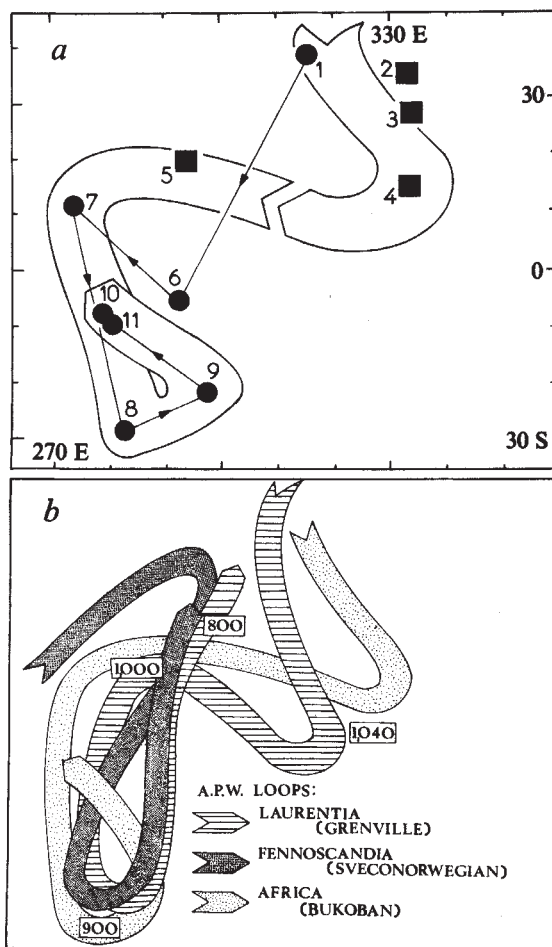
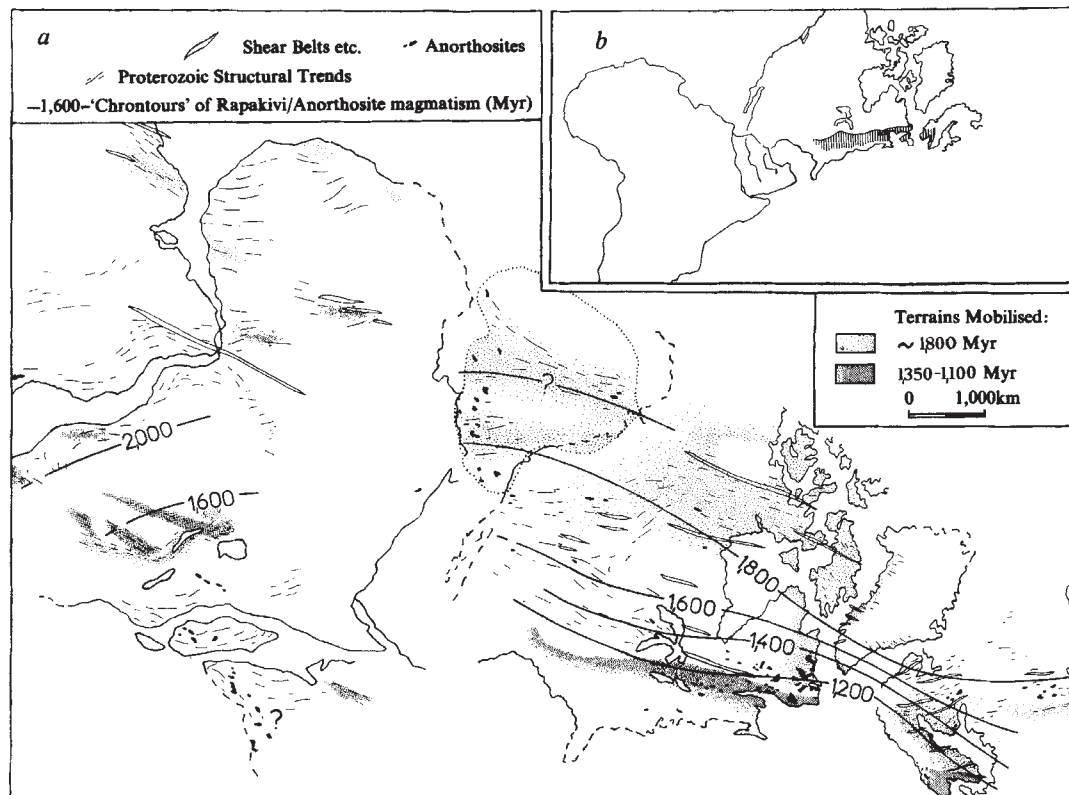


Fig. 2 *a*, African 1,050–800 Myr palaeomagnetic poles^{5,15} from margins of the Tanganyika (●) and Kalahari (■) Shields with assigned ages in brackets: 1, Bukoba sandstone (1,000 Myr); 2, Chela sediments; 3, Nosib quartzite; 4, O'okiep intrusives (1,047 Myr); 5, Klein Karas dykes (>890 Myr); 6, Malagarasi sandstone; 7, Kigonero flags (900–1,000 Myr); 8, Gagwe lavas (818 Myr); 9, Manyovu red beds; 10, Moala dolerites; 11, Bukoban dolerites (811 Myr). The dashed line connects the sequence of poles defined from the stratigraphic succession of the Bukoban System; there is overlap between 95% confidence ovals of some of these poles. For pre-1,040 Myr data see ref. 25. *b*, Comparison in size and shape of the three APW loops.

Fig. 3 *a*, The distribution of some of the major shields in Middle Proterozoic times after refs 20, 25, 26 compared with the reconstruction (*b*) derived by superimposing the three 1,050–800 Myr APW loops of Figs 1 and 2. The configuration of the Siberian Shield in *a* is that proposed by Sears and Price³⁶; present palaeomagnetic data are not in conflict with this reconstruction²⁶ but are not yet suitable for a definitive test. The distribution of some major geological features formed between ~2,700 and 1,100 Myr is plotted on *a*, and the chrontours define the approximate time of termination of anorogenic intrusive magmatism belonging to the massive anorthosite/rapakivi granite suite.



at ~1,100 Myr represent the earliest phase in disruption of a consolidating Proterozoic crust? Present palaeomagnetic data bearing on this point are equivocal, although they are consistent with a single configuration of the Fennoscandian and Laurentian Shields to at least 1,700 Myr (refs 25, 26) (and the African and Laurentian Shields to at least 2,100 Myr (ref. 25)). There is, however, a strong geological case to suggest that the crustal distribution of Fig. 3*a* represents the approximate form of the continental crust before ~1,100 Myr (the Australian sector of Gondwanaland is omitted from this diagram because relative motions before the Lower Palaeozoic²⁷ leave uncertainties about its relationship to the other shields). This evidence includes the general alignment of Lower Proterozoic structural trends, mylonite and strike-slip zones^{26,26-30} and the pattern of the Rapakivi-massive anorthosite intrusive activity. Conditions appropriate³¹ to this anorogenic magmatism, widespread in early Proterozoic times, became progressively more restricted within the zones regenerated during the widespread ~1,800 Myr mobile activity (ref. 32 and Fig. 3*a*) with a gradual restriction to one margin of the Fennoscandian-Laurentian Shield; intrusion ceased altogether at about 1,000 Myr. Figure 3 shows 'chrontours' (based mainly on age data compilations discussed in refs 32 and 26) to describe the contraction of this magmatism across the Proterozoic crust. These appear to reflect declining temperature gradients as this crustal unit cooled so that conditions were no longer appropriate to the high level intrusion of large anorogenic bodies; a comparable trend seems to be present across the African Shield (Fig. 3*a*), although the data points here are too few to be sure of this.

The intrusion of anorogenic bodies persisted longest near the Grenville and Sveconorwegian mobile belts. These and other belts formed during the episode of mobile activity at 1,350–1,100 Myr (ref. 33) tend to form linear and relatively narrow zones separated by sharp structural and/or thermal contacts from adjoining terrains; they are probably more widespread than originally suspected within the African Shield³⁴. Their alignment along a great circle trend¹⁶ in the pre-1,100 Myr reconstruction (Fig. 3*a*) began to be dismembered by the post-1,100 Myr motions (Fig. 3*b*)).

Therefore, the initial break-up of the sialic crust apparently followed closely on the decline of temperature gradients defined

by the stage at which anorogenic magmatism could no longer take place outside narrow zones of crustal mobility. This stage is also represented by transcontinental brittle fracturing during the Mackenzie-Sudbury-Gardar-Jotnian igneous episode at ~1,200 Myr (ref. 20). The transition to the scheme of plate tectonics characteristic of Phanerozoic times was, however, a gradual one because ensialic zones of crustal mobility were still developing within the African Shield at 700–500 Myr (ref. 35).

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Oxygen isotopic-hydrographic relationships among recent planktonic Foraminifera from the Indian Ocean

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The stable isotopic composition of fossil Foraminifera has become an increasingly important tool in palaeoecological and stratigraphic studies of marine sediments¹⁻³, prompting several studies of the factors governing the isotopic composition of living and recent Foraminifera. Many studies have documented the good agreement between the inferred depth of growth from oxygen isotopic data⁴⁻⁸ and the depth stratification found in plankton tows⁹⁻¹¹. Although results have suggested disequilibrium in some species¹²⁻¹⁴, especially among the benthic species^{15,16}, recent data from Sargasso Sea plankton tows¹⁷⁻¹⁹ and Indian Ocean core top sediments^{20,21} suggest that oxygen isotopic equilibrium is nearly achieved in many ecologically important species. In the present study, oxygen isotopic data on as many as eight species and subspecies of planktonic Foraminifera from 52 Indian Ocean core top samples permit a comprehensive comparison of the isotopic-temperature trends across the major oceanographic regions of the Indian Ocean (Table 1). Several shallow-dwelling species (*Globigerinoides ruber*, *G. sacculifer* and *Orbulina universa*) were used as a measure of the upper 50–100 m of the water column (the mixed surface layer). Several deep-dwelling species (*G. truncatulinoides* (left and right coiling varieties), *G. inflata*, *G. scitula* and *G. hirsuta*) were used for comparison with hydrographic data from 200 to 300 m depths. The results show that the isotopic difference between the shallow and deep-dwelling species is directly related to the temperature difference between the surface waters and the depth of the permanent thermocline. This isotopic-temperature relationship suggests that isotopic analyses of species which inhabit different water depths may be used to determine the thermal gradient in the upper water column during the Cenozoic.

The foraminiferal $\delta^{18}\text{O}$ data are from four sources: widely distributed core tops from Williams⁸ and Prell *et al.*²²; Arabian Sea and Bay of Bengal core tops from Duplessy²³; and core tops from the southwestern Indian Ocean by Shackleton and Vincent²⁴. Temperature and salinity data were obtained for each core top location from the Indian Ocean atlas of Wyrki²⁵ and surface temperature maps compiled by the Geophysical Fluid Dynamics Laboratory²⁶ (Table 1). The salinity- $\delta^{18}\text{O}$ relationship for Indian Ocean waters was used to estimate the isotopic composition of seawater²⁷. The isotopic equilibrium relationship of inorganically precipitated calcite²⁸ was used to estimate the $\delta^{18}\text{O}$ of calcite precipitated in isotopic equilibrium at ambient seawater conditions. Linear regression analyses were then used to compare the foraminiferal isotopic data against surface water temperature, and the $\delta^{18}\text{O}$ of equilibrium calcite at 0, 200 and 300 m.

Strong linear correlations exist between the $\delta^{18}\text{O}$ of the shallow dwelling species, surface-water temperature and estimated $\delta^{18}\text{O}$ values for equilibrium calcite at surface conditions (Fig. 1; Table 2). The isotopic composition of the three mixed surface layer species shows depleted values at warmer water temperatures and a steady enrichment at colder temperatures.

Individually, the $\delta^{18}\text{O}$ of *G. ruber* and *O. universa* have the best fit with average surface temperature ($r = -0.89$ and -0.91). Collectively, the $\delta^{18}\text{O}$ values of all three species have an equally strong correlation with average surface temperature ($r = -0.89$). The slope and intercept of the regression equations are almost identical to those based on equilibrium calcite values and temperature at the same locations (Table 2). The differences in slope and intercept of the regression results for each species (Table 2) reflect the slight differences in calcification temperature due either to seasonal growth or to small depth habitat differences within the mixed surface layer.

Over the same latitudinal and temperature range, however, the isotopic composition of the deep-dwelling *Globorotalia* species shows very little systematic change (Fig. 1). North of the Subtropical Convergence (STC) zone (38° – 42° S) the $\delta^{18}\text{O}$ -temperature gradient for the four *Globorotalia* species together ($r = -0.53$) is $0.05\% \text{ } ^{\circ}\text{C}^{-1}$, <30% of the gradient exhibited in the shallow species and equilibrium calcite. The oxygen isotopic composition of *G. inflata* and *G. truncatulinoides* has a poor correlation with surface temperature ($r = -0.54$ and -0.62). Assuming isotopic equilibrium, calcification among the *Globorotalia* group north of the STC seems to occur at the base of the seasonal thermocline between 200 and 300 m on the basis of estimated $\delta^{18}\text{O}$ values for equilibrium calcite at these depths (Fig. 1). South of the STC, the $\delta^{18}\text{O}$ of the *Globorotalia* species becomes significantly correlated with surface temperature ($r = -0.89$) with an increase in the $\delta^{18}\text{O}$ -temperature gradient to $0.13\% \text{ } ^{\circ}\text{C}^{-1}$ (Fig. 1; Table 2). Individually, *G. truncatulinoides* and *G. inflata* specimens south of the STC exhibit equally strong correlations between their isotopic composition and temperature ($r = -0.93$ and -0.97) (Table 2).

These isotopic trends among the shallow and deep dwelling foraminiferal species have an oceanographic explanation which has important implications for future palaeoceanographic studies. In northern subtropical, equatorial and southern subtropical waters where a steep thermocline exists either year-round or seasonally, the temperature dependent isotopic difference between the deep and shallow dwelling species ($\Delta^{18}\text{O} = \delta^{18}\text{O}_{\text{deep}} - \delta^{18}\text{O}_{\text{shallow}}$) is large and varies between 3.7 and 1.5‰ (Figs 1 and 2). $\Delta^{18}\text{O}$ undergoes a systematic decrease toward higher latitudes and decreasing surface water temperature, mirroring the change in the temperature gradient between the surface and depth of the permanent thermocline. At the STC zone, where southern subtropical and northern subantarctic surface water masses converge, $\Delta^{18}\text{O}$ reaches a minimum of <1‰, corresponding to the region where the thermocline has a minimal thermal gradient. In the subantarctic, $\Delta^{18}\text{O}$ remains at a minimum, reflecting the lack of a temperature difference between either the season of growth or depth of growth of the deep and shallow species of this region. The same basic $\Delta^{18}\text{O}$ -temperature relationship exists if the isotopic difference between the *Globorotalia* group and *G. ruber*, or *G. truncatulinoides* and *G. ruber* is used (Fig. 2).

By calibrating these systematic isotopic differences between pelagic species which inhabit the mixed surface layer and the upper permanent thermocline, the isotopic difference between the average $\delta^{18}\text{O}$ values of the shallow species and deep *Globorotalia* species could be used to provide an average measure of the temperature difference between the mixed layer and permanent thermocline during different climatic and glaciological states. Likewise, the isotopic difference between a single shallow species (*G. ruber*) and deep species (*G. truncatulinoides*) which have overlapping geographic ranges, could also be utilised. Although all three of the $\Delta^{18}\text{O}$ -temperature relationships are strongly linear (Table 3), the best fit lines are not parallel but converge towards lower temperatures (Fig. 2). At a temperature maximum of 28°C , the $\Delta^{18}\text{O}$ -temperature equations differ by only $\pm 0.25\%$ (1 s.d.), which is equivalent to a temperature difference of $\pm 1.2^{\circ}\text{C}$ (1 s.d.). An estimated error in the $\Delta^{18}\text{O}$ (deep-shallow) equation of $\pm 0.33\%$ ($\pm 1.65^{\circ}\text{C}$) is obtained by comparing observed and estimated $\Delta^{18}\text{O}$ values. Although more time consuming, the use of an average isotopic

Fig. 1 Linear regression results comparing the $\delta^{18}\text{O}$ of the shallow ($\circ$) species (*G. ruber*, *G. sacculifer*, *O. universa*) and deep ($\bullet$) species (*G. truncatulinoides*, *G. inflata*, *G. hirsuta*, *G. scitula*) to average surface-water temperature in the Indian Ocean. The temperature range of the subtropical convergence zone (STC) is indicated. The solid lines 1, 3, and 6 represent the best fit lines for all shallow species, all deep species north of the STC, and all deep species south of the STC, respectively (Table 2). The dashed lines represent the best fit lines for equilibrium calcite at 0 m (2), 200 m (4, north of the STC; 7, south of the STC) and 300 m (5, north of the STC) (Table 2). The size fraction of the foraminiferal specimens varied from $>63\ \mu\text{m}$ (ref. 24) to $>150\ \mu\text{m}$ (refs 8, 22, 23). The isotopic differences between different size fractions of the same species^{33,34} probably add to the scatter in the data but do not detract from the results of this study.

Other essential aspects of the analytical techniques were the same in generating the isotopic data: monospecific foraminiferal calcite samples were reacted *in vacuo* in purified phosphoric acid after roasting *in vacuo* for 1 h. The evolved CO_2 gas was purified of water vapour and analysed in a VG Micromass 602 mass spectrometer. All are reported in the conventional δ notation as the $\%$ enrichment or depletion in ^{18}O relative to the PDB standard³⁵. Detailed analytical procedures can be found in Shackleton and Opdyke³⁶, Williams *et al.*³⁷ and Duplessy²³. Oxygen isotope stratigraphy was used to validate the age of nearly all the core top samples as Recent or late Holocene.

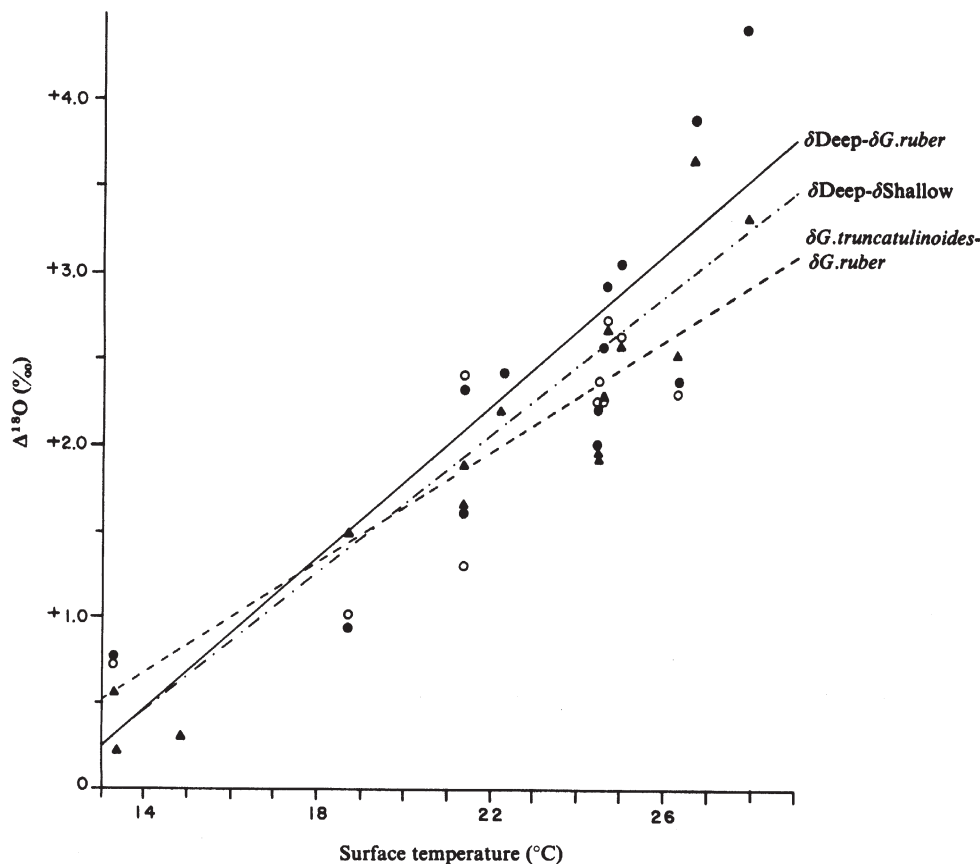
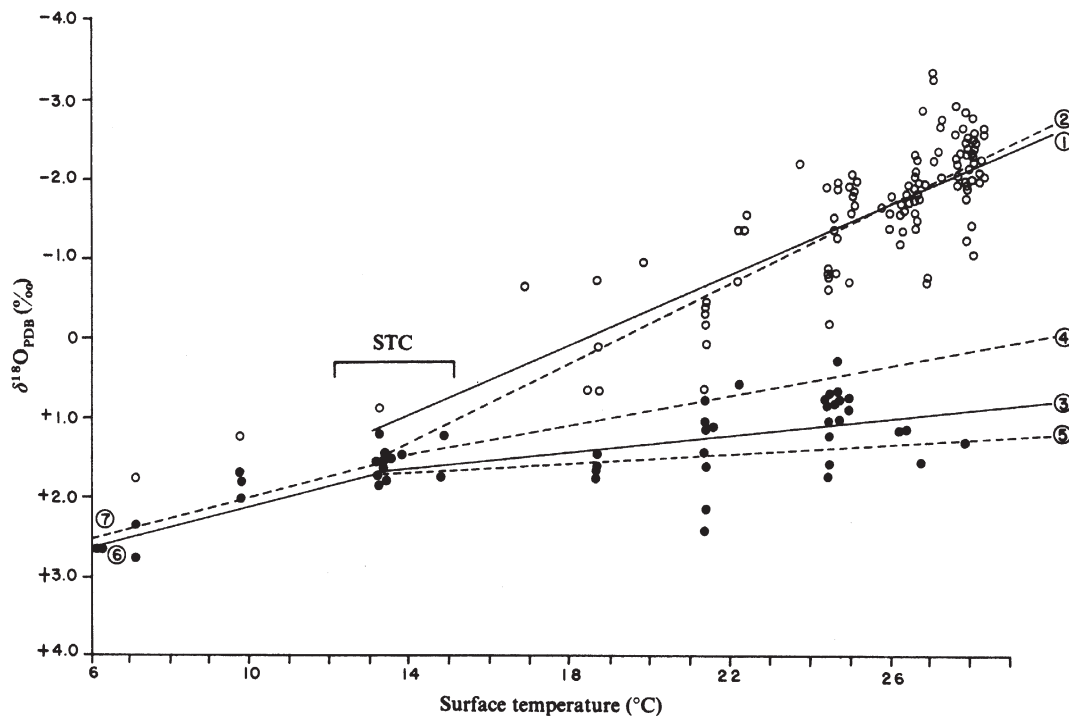


Fig. 2 Linear regression results comparing the oxygen isotopic difference ($\Delta^{18}\text{O}$) of average deep-shallow group ($\blacktriangle$), average deep group - *G. ruber* ($\bullet$), and *G. truncatulinoides* - *G. ruber* ($\circ$) with surface water temperature. See Table 3 for exact equations.

Table 1 Foraminiferal, salinity and temperature data

Species	$\delta^{18}\text{O}_{\text{PDB}}$	$\delta^{13}\text{C}_{\text{PDB}}$	Core top	Lat	Long	Surface temperature (°C)*	Surface salinity†	$\delta^{18}\text{O}_{\text{w}}\ddagger$	Source
<i>Globigerinoides ruber</i>	-1.96	+1.10	366B	23°09' S	48°08' E	24.70	35.25	0.40	24
	-1.86	+0.68	363C	23°45' S	43°10' E	25.00	35.25	0.40	24
	-1.51	+0.58	361J	25°31' S	37°45' E	24.60	35.30	0.40	24
	-1.38	+1.00	389B	30°10' S	32°04' E	22.25	35.45	0.49	24
	-0.16	+0.23	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	-1.54	+1.05	V14-101B	08°39' N	58°34' E	26.00	35.18	0.42	23
	-1.98	+1.12	V14-104	13°26' N	53°27' E	25.15	35.70	0.73	23
	-2.23	+1.24	V14-107	11°51' N	46°45' E	26.70	35.95	0.73	23
	-2.57	+0.76	RC9-155	07°24' N	72°48' E	28.10	35.00	0.06	23
	-2.33	+1.19	RC12-328	08°57' N	60°36' E	27.25	35.15	0.20	23
	-1.44	+0.39	RC12-331	02°30' N	69°52' E	28.1	35.10	0.40	23
	-2.47	+0.89	RC17-126	07°00' N	72°00' E	27.95	34.50	-0.18	23
	-2.04	+1.20	V19-176	07°07' N	76°33' E	27.75	33.85	-0.66	23
	-2.37	+0.99	V19-177	07°35' N	74°13' E	27.95	34.25	-0.52	23
	-2.84	+0.89	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	23
	-2.89	+1.16	V19-183	08°07' N	62°47' E	26.85	35.30	0.16	23
	-2.31	+0.97	V19-185	06°42' N	59°20' E	26.65	35.25	0.20	23
	-1.82	+1.04	V19-188	06°52' N	60°40' E	26.65	35.25	0.20	23
	-2.65	+1.12	RC12-339	09°08' N	90°02' E	27.95	33.80	-0.37	23
	-2.93	+0.95	RC12-340	12°42' N	90°01' E	27.70	33.35	-0.66	23
	-2.77	+1.11	RC12-341	13°03' N	80°35' E	27.35	33.50	-0.66	23
	-3.36	+0.92	RC12-344	12°46' N	96°04' E	27.10	32.05	-0.34	23
	-2.78	+0.90	RC12-347	09°20' N	93°20' E	28.10	33.50	-0.66	23
	-2.66	+0.92	RC14-36	0°28' S	90°00' E	28.35	34.23	-0.08	23
	-2.42	+1.08	RC14-39	05°51' N	90°31' E	27.95	33.85	-0.42	23
	-2.55	+1.35	RC14-44	05°58' S	102°27' E	27.65	32.00	-1.14	23
	-2.45	+0.41	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	8
	-1.82	+0.86	V19-185	06°42' N	59°20' E	26.65	35.25	0.20	8
	-1.17	+0.61	V19-202	06°59' S	41°11' E	26.35	35.20	0.35	8
	-2.03	+0.78	RC11-147	19°04' S	112°45' E	25.05	34.95	0.30	8
	-0.79	+0.02	V20-170	21°48' S	69°14' E	24.50	34.85	0.06	8
	-0.86	+0.14	V20-175	22°18' S	68°00' E	24.50	34.85	0.06	8
	-0.27	+0.00	V18-207	25°38' S	87°07' E	21.40	34.95	-0.04	8
	+0.68	+0.36	RC11-126	30°04' S	94°25' E	18.75	35.85	0.73	8
	+0.90	+0.49	E48-22A	39°54' S	85°25' E	13.3	35.08	0.32	8
	-1.90	+0.42	RC12-339	09°08' N	90°02' E	27.85	34.13	-0.06	8
	+0.67	—	E48-11	29°40' S	97°32' E	18.45	35.90	0.73	22
	-1.67	—	V19-202	06°41' S	41°11' E	26.35	35.20	0.35	22
	-1.58	—	V19-202	06°41' S	41°11' E	26.35	35.20	0.35	22
<i>Globigerinoides sacculifer</i>	-1.86	+1.29	366B	23°09' S	48°08' E	24.7	35.25	0.40	24
	-1.58	+1.75	363C	23°45' S	43°10' E	25.0	35.25	0.40	24
	-1.37	+1.60	361J	25°31' S	37°45' E	24.6	35.30	0.40	24
	-1.37	+2.02	389B	30°10' S	32°04' E	22.25	35.45	0.49	24
	-0.38	+1.30	379B	32°23' S	42°56' E	21.4	35.50	0.54	24
	-1.37	+1.77	V14-101B	08°39' N	58°34' E	26.0	35.18	0.42	23
	-1.69	+2.08	V14-104	13°26' N	53°27' E	25.15	35.70	0.73	23
	-1.66	+1.30	DAL7-60	23°15' N	61°28' E	25.80	36.45	1.12	23
	-1.57	+1.70	V14-107	11°51' N	46°45' E	26.7	35.95	0.73	23
	-2.20	+1.57	RC9-155	07°24' N	72°48' E	28.1	35.00	0.06	23
	-2.02	+1.83	RC12-328	03°57' N	60°36' E	27.25	35.15	0.20	23
	-1.04	+1.46	RC12-331	02°30' N	69°52' E	28.1	35.10	0.40	23
	-1.75	+1.78	RC17-126	7°00' N	72°00' E	27.95	34.50	-0.18	23
	-2.34	+1.50	V19-176	7°07' N	76°33' E	27.75	33.85	-0.66	23
	-2.13	+1.47	V19-177	07°35' N	74°13' E	27.95	34.25	-0.52	23
	-1.95	+1.79	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	23
	-1.94	+1.55	V19-183	08°07' N	62°47' E	26.85	35.30	0.16	23
	-2.03	+1.67	V19-185	06°42' N	59°20' E	26.65	35.25	0.20	23
	-1.74	+1.70	V19-188	06°52' N	60°40' E	26.65	35.25	0.20	23
	-2.31	+1.53	RC12-339	09°08' N	90°02' E	27.95	33.80	-0.37	23
	-2.18	+1.55	RC12-340	12°42' N	90°01' E	27.7	33.35	-0.66	23
	-2.68	+1.65	RC12-341	13°03' N	80°35' E	27.35	33.50	-0.66	23
	-3.26	+1.59	RC12-344	12°46' N	96°04' E	27.1	32.05	-1.34	23
	-2.27	+1.51	RC12-347	09°20' N	93°20' E	28.1	33.50	-0.66	23
	-2.24	+1.60	RC14-36	0°28' S	90°00' E	28.35	34.23	-0.08	23
	-2.45	+1.52	RC14-39	05°51' N	90°31' E	27.95	33.85	-0.42	23
	-2.26	+1.87	RC14-44	05°58' S	102°27' E	27.65	32.0	-1.14	23
	-1.88	+1.44	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	8
	-1.73	+1.64	V19-185	06°42' N	59°20' E	27.65	35.25	0.20	8
	-1.54	+1.97	V19-202	06°59' S	41°11' E	26.35	35.20	0.35	8
	-1.86	+1.99	RC11-147	19°04' S	112°45' E	25.05	34.95	0.30	8
	-0.73	+1.32	V20-170	21°48' S	69°14' E	24.5	34.85	0.06	8
	-0.77	+1.28	V20-175	22°18' S	68°00' E	24.5	34.85	0.06	8
	-0.41	+1.12	V18-207	25°38' S	87°07' E	21.4	34.95	-0.04	8
	-0.71	+1.13	RC11-126	30°04' S	94°25' E	18.75	35.85	0.73	8
	-1.97	+1.97	RC12-339	09°08' N	90°02' E	27.85	34.13	-0.37	8
	-1.75	—	V14-101B	08°39' N	58°34' E	26.00	35.35	0.42	22
	-2.22	—	RC14-29	10°55' S	88°19' E	27.10	34.20	0.01	22
	-2.01	—	RC14-35	0°50' S	89°57' E	28.35	34.18	-0.13	22
	-2.56	—	RC14-35	0°50' S	89°57' E	28.35	34.18	-0.13	22
	-2.09	—	RC14-37	01°28' N	90°10' E	28.25	34.15	-0.18	22
	-1.98	—	RC14-37	01°28' N	90°10' E	28.25	34.15	-0.18	22
	-1.88	—	RC11-147	19°04' S	112°45' E	24.46	34.95	0.30	22
	-1.56	—	V19-204	10°14' S	43°49' E	26.65	35.15	0.30	22

* See ref. 26. † See ref. 25.

‡ Oxygen isotopic composition of seawater using the salinity/ $\delta^{18}\text{O}$ relationship for the Indian Ocean²⁷.

Table 1—continued

Species	$\delta^{18}\text{O}_{\text{PDB}}$	$\delta^{13}\text{C}_{\text{PDB}}$	Core top	Lat	Long	Surface temperature (°C)*	Surface salinity†	$\delta^{18}\text{O}_w\ddagger$	Source
<i>Globigerinoides sacculifer</i> (continued)	-1.37	—	V19-204	10°14' S	43°49' E	26.65	35.15	0.30	22
	-0.69	—	V29-48	06°16' S	63°26' E	26.95	34.80	0.20	22
	-0.71	—	V29-48	06°16' S	63°26' E	26.95	34.80	0.20	22
	-1.95	—	V19-185	06°42' S	59°20' E	26.65	35.25	0.20	22
	-2.04	—	V19-185	06°42' S	59°20' E	26.65	35.25	0.20	22
	-1.55	—	RC17-69	31°30' S	32°36' E	22.40	35.40	0.49	22
	-2.30	—	V29-30	03°05' N	76°15' E	28.10	35.00	0.30	22
	-1.97	—	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	22
	-2.20	—	RC9-161	19°34' N	59°36' E	23.75	36.15	0.97	22
	-1.91	—	RC17-98	13°13' S	65°37' E	26.55	34.65	0.11	22
	-1.72	—	RC17-98	13°13' S	65°37' E	26.55	34.65	0.11	22
	-0.65	—	RC11-86	35°47' S	18°27' E	16.95	35.00	0.30	22
	-0.95	—	RC9-150	31°17' S	114°33' E	19.85	35.85	0.69	22
	-2.44	—	V29-29	05°07' N	77°35' E	28.00	34.70	0.06	22
<i>Orbulina unioersa</i>	-1.24	+1.88	366B	23°09' S	48°08' E	24.70	35.15	0.40	24
	-0.71	+1.91	363C	23°45' S	43°10' E	25.00	35.15	0.40	24
	-0.80	+1.73	361J	25°31' S	37°45' E	24.60	35.20	0.40	24
	-0.70	+1.56	389B	30°10' S	32°04' E	22.25	35.45	0.49	24
	+0.64	+1.36	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	-1.22	+0.55	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	8
	-1.91	+2.06	V19-185	06°42' N	59°20' E	26.65	35.25	0.20	8
	-1.34	+1.68	V19-202	06°59' N	41°11' E	26.35	35.20	0.35	8
	-1.79	+1.76	RC11-147	19°04' S	112°45' E	25.05	34.95	0.30	8
	-0.59	+1.75	V20-170	21°48' S	69°14' E	24.50	34.85	0.06	8
	-0.18	+1.66	V20-175	22°18' S	68°00' E	24.50	34.85	0.06	8
	+0.06	+1.73	V18-207	25°38' S	87°07' E	21.40	34.95	-0.04	8
	+0.11	+1.84	RC11-126	34°04' S	94°25' E	18.75	35.85	0.73	8
	+1.22	+1.60	E48-27A	38°32' S	79°54' E	14.85	35.30	0.49	8
	+1.41	+1.73	E48-23A	39°31' S	83°43' E	13.40	35.10	0.35	8
	+1.16	+1.60	E48-22A	39°54' S	85°25' E	13.30	35.08	0.32	8
	+1.24	+1.20	RC11-120	43°31' S	79°52' E	9.80	34.75	0.06	8
	+1.63	+1.73	E45-73A	47°33' S	114°26' E	7.20	34.50	0.06	8
<i>Globorotalia scitula</i>	+0.30	—	366B	23°09' S	48°08' E	24.70	35.25	0.04	24
	+1.06	-1.16	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	+1.32	-0.17	V19-178	08°07' N	73°15' E	27.95	34.70	-0.23	8
	+1.58	+0.72	V19-185	06°42' N	59°20' E	26.80	35.25	0.20	8
	+1.19	-0.15	V19-202	06°59' S	41°11' E	26.35	35.25	0.35	8
	+1.80	-0.46	RC11-126	30°04' S	94°25' E	13.75	35.85	0.73	8
	+1.77	-0.22	E48-22A	39°54' S	85°25' E	13.30	35.08	0.32	8
	+1.74	-0.04	RC11-120	43°31' S	79°52' E	9.80	34.75	0.06	8
<i>Globorotalia truncatulinoides</i> (L)	+0.72	+1.26	366B	23°09' S	48°08' E	24.70	35.25	0.40	24
	+0.77	+1.36	363C	23°45' S	43°10' E	25.00	35.25	0.40	24
	+0.73	+1.41	361J	25°31' S	37°04' E	24.60	35.30	0.40	24
	+0.81	+0.97	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	+0.84	+1.22	V20-170	21°48' S	69°14' E	24.50	34.85	0.06	8
	+1.05	+1.35	V20-175	22°18' S	68°00' E	24.50	34.85	0.06	8
	+1.65	+0.88	RC11-126	30°04' S	94°25' E	18.75	35.85	0.73	8
	+1.47	+0.47	E48-27A	38°32' S	79°54' E	14.85	35.30	0.49	8
	+1.69	+0.34	E48-23A	39°31' S	83°43' E	13.40	35.10	0.35	8
	+1.61	+0.43	E48-22A	39°54' S	85°25' E	13.30	35.08	0.32	8
	+1.78	+0.78	RC11-120	43°31' S	79°52' E	9.80	34.75	0.06	8
	+2.40	+1.13	E45-73A	47°33' S	114°26' E	7.20	34.50	0.06	8
	+2.69	+1.14	RC8-63	51°05' S	129°58' E	6.10	34.00	-0.18	8
	+1.87	—	E48-22A	39°53' S	85°25' E	13.30	35.08	0.32	22
	+1.61	—	E48-22A	39°53' S	85°25' E	13.30	35.08	0.32	22
<i>Globorotalia truncatulinoides</i> (R)	+0.78	+1.07	366B	23°09' S	48°08' E	24.70	35.25	0.04	24
	+0.75	+1.06	361J	25°31' S	37°04' E	24.60	35.30	0.04	24
	+1.12	+0.86	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	+1.12	+0.61	V19-202	06°59' S	41°11' E	26.35	35.20	0.35	8
	+1.58	+1.10	V20-170	21°48' S	69°14' E	24.50	34.85	0.06	8
	+1.72	+1.39	V20-175	22°18' S	68°00' E	24.50	34.85	0.06	8
	+2.15	+1.37	V18-207	25°38' S	87°07' E	21.40	34.95	-0.04	8
	+1.71	+0.92	RC11-126	30°04' S	94°25' E	18.75	34.85	0.73	8
<i>Globorotalia hirsuta</i>	+1.45	+0.68	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	+2.44	+1.11	V18-207	25°38' S	87°07' E	21.40	34.95	-0.04	8
	+1.79	+0.88	E48-27A	38°32' S	79°54' E	14.85	35.30	0.49	8
	+1.58	+0.96	E48-23A	39°31' S	83°43' E	13.40	35.10	0.35	8
	+1.84	+1.41	E48-22A	39°54' S	85°25' E	13.30	35.08	0.32	8
<i>Globorotalia inflata</i>	+1.04	+0.62	366B	23°09' S	48°08' E	24.70	35.25	0.40	24
	+0.92	+0.91	363C	23°45' S	43°10' E	25.00	35.25	0.40	24
	+0.74	+0.78	361J	25°31' S	37°04' E	24.60	35.30	0.40	24
	+0.61	+0.48	389B	30°10' S	32°04' E	22.25	35.45	0.49	24
	+1.16	+0.24	379B	32°23' S	42°56' E	21.40	35.50	0.54	24
	+1.26	+0.47	V20-175	22°18' S	68°00' E	24.50	34.85	0.06	8
	+1.65	+0.74	V18-207	25°38' S	87°07' E	21.40	34.95	-0.04	8
	+1.46	+0.59	RC11-126	30°04' S	94°25' E	18.75	35.85	0.73	8
	+1.31	+0.60	E48-27A	38°32' S	79°54' E	14.85	35.30	0.49	8
	+1.55	+0.38	E48-23A	39°31' S	83°43' E	13.40	35.10	0.35	8
	+1.25	+0.62	E48-22A	39°54' S	85°25' E	13.30	35.08	0.32	8
	+2.06	+1.15	RC11-120	43°31' S	79°52' E	9.80	35.75	0.06	8
	+2.84	+1.21	E45-73A	47°33' S	114°26' E	7.20	34.50	0.06	8
	+2.69	+1.14	RC8-63	51°05' S	129°58' E	6.10	34.00	-0.18	8

composition for the deep and shallow group would have the advantage of minimising preferential biasing of the isotopic record by bioturbation effects on a single species which undergoes changing relative abundances through short-term climatic cycles²⁹.

In addition, the results of this study show that the change in the latitudinal $\Delta^{18}\text{O}$ -temperature gradient in *G. truncatulinoides* and *G. inflata* north and south of the STC can be used to detect changes in the past positions of water mass boundaries such as the STC (the $\delta^{18}\text{O}$ of *G. truncatulinoides* changes from 0.06 to 0.12‰ °C⁻¹ and the $\delta^{18}\text{O}$ of *G. inflata* changes from 0.04 to 0.19‰ °C⁻¹ north and south of the STC, respectively). In fossil assemblages where *G. truncatulinoides* is rare or absent, other abundant deep dwelling species such as *G. inflata* may be substituted. South of the STC, the $\delta^{18}\text{O}$ -temperature best fit line for all the deep dwelling species parallels the best fit lines for equilibrium calcite at both the surface and 200 m.

The $\Delta^{18}\text{O}$ trends in the Indian Ocean surface sediments strongly suggest that seasonality may also be recorded in the isotopic composition of fossil assemblages. Results of an isotopic study of living *G. ruber* and *G. truncatulinoides* collected seasonally in the Sargasso Sea¹⁷ have shown that the observed isotopic difference ($\Delta^{18}\text{O}$) between *G. ruber* during the summer temperature maximum and *G. truncatulinoides* during the winter temperature minimum ($\Delta^{18}\text{O} = 2.0\%$) agrees remarkably well with the estimated $\Delta^{18}\text{O}$ of 2.18‰. This estimated $\Delta^{18}\text{O}$ value was obtained by extrapolating the average surface temperature at the Sargasso Sea location (23.4 °C) to the $\Delta^{18}\text{O}$ -temperature relationship for *G. truncatulinoides* and *G. ruber* in the Indian Ocean (Fig. 2). These results suggest that the isotopic composition of certain planktonic foraminiferal species is both a function of depth habitat (particularly in equatorial regions where little seasonal change in the thermocline occurs) and seasonal occurrence.

Of course, to use the modern interglacial $\Delta^{18}\text{O}$ relationship to estimate absolute sea-surface temperatures during the Pleistocene, it must be assumed that the deep dwelling species maintain approximately the same mean calcification temperature during glacial times. The near constant isotopic composition of *Globorotalia* species from such widely different oceanographic regions as the Arabian Sea to the Subtropical Convergence suggests that this assumption may be reasonable. It has already been shown that surface isotherms during the last glacial maximum can be reconstructed using the isotopic composition of *G. sacculifer* at equivalent levels in piston cores³⁰. It may therefore

Table 3 Linear regression analyses of foraminiferal isotopic differences and water temperature

$\delta^{18}\text{O}$	Temperature	Correlation coefficient	Least squares equation
Deep-shallow*	0 m	0.94	$\Delta^{18}\text{O} = -2.35 + 0.20T$
Deep-shallow*	$\Delta T^\dagger$, 0-200 m	0.88	$\Delta^{18}\text{O} = 0.21 + 0.25\Delta T$
Deep- <i>G. ruber</i> ‡	0 m	0.85	$\Delta^{18}\text{O} = -2.62 + 0.22T$
Deep- <i>G. ruber</i> ‡	$\Delta T^\dagger$, 0-200 m	0.82	$\Delta^{18}\text{O} = 0.49 + 0.25\Delta T$
<i>G. trunc.</i> - <i>G. ruber</i> §	0 m	0.87	$\Delta^{18}\text{O} = -1.56 + 0.16T$
<i>G. trunc.</i> - <i>G. ruber</i> §	$\Delta T^\dagger$, 0-200 m	0.70	$\Delta^{18}\text{O} = 0.73 + 0.19\Delta T$

* Deep-shallow = ($\delta^{18}\text{O}$ of *G. truncatulinoides* + *G. inflata* + *G. scitula* + *G. hirsuta*) - ($\delta^{18}\text{O}$ of *G. ruber* + *G. sacculifer* + *O. universa*).

† $\Delta T = T_{0m} - T_{200m}$.

‡ Deep-*G. ruber* = $\delta^{18}\text{O}$ of deep group - $\delta^{18}\text{O}$ of *G. ruber*.

§ $\delta^{18}\text{O}$ of *G. truncatulinoides* - $\delta^{18}\text{O}$ of *G. ruber*.

be possible to map the geographic distribution of $\Delta^{18}\text{O}$ at different times to determine the changes in the thermal gradient of the upper water column and to provide a comparison with sea-surface temperature estimates based on micropalaeontological transfer functions^{31,32}. In addition, the correspondence between the $\Delta^{18}\text{O}$ trend in surface sediments of the Indian Ocean and the seasonal temperature-isotopic relationship in the Sargasso Sea suggests that the seasonality of a region may be decipherable from isotopic studies of multiple species from fossil assemblages.

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Table 2 Linear regression analyses of foraminiferal isotopic composition versus water temperature

$\delta^{18}\text{O}^*$	Surface temperature†	Correlation coefficient	Least squares equations
<i>G. ruber</i>	0 m	-0.89	$\delta^{18}\text{O} = 5.48 - 0.28T$
<i>G. ruber</i>	Aug., 0 m	-0.91	$\delta^{18}\text{O} = 3.80 - 0.22T$
<i>G. ruber</i>	Feb., 0 m	-0.77	$\delta^{18}\text{O} = 6.58 - 0.32T$
<i>G. sacculifer</i>	0 m	-0.66	$\delta^{18}\text{O} = 2.36 - 0.16T$
<i>O. universa</i>	0 m	-0.91	$\delta^{18}\text{O} = 3.30 - 0.17T$
Shallow‡	0 m	-0.86	$\delta^{18}\text{O} = 4.03 - 0.22T$
Deep§, N of STC	0 m	-0.53	$\delta^{18}\text{O} = 2.35 - 0.05T$
Deep§, S of STC	0 m	-0.89	$\delta^{18}\text{O} = 3.42 - 0.13T$
<i>G. trunc.</i> , N of STC	0 m	-0.62	$\delta^{18}\text{O} = 2.55 - 0.06T$
<i>G. trunc.</i> , S of STC	0 m	-0.93	$\delta^{18}\text{O} = 3.28 - 0.12T$
<i>G. inflata</i> , N of STC	0 m	-0.54	$\delta^{18}\text{O} = 1.96 - 0.04T$
<i>G. inflata</i> , S of STC	0 m	-0.97	$\delta^{18}\text{O} = 3.95 - 0.19T$
equil , 0 m	0 m	-0.94	$\sigma^{18}\text{O} = 4.81 - 0.25T$
equil , 200 m, N of STC	0 m	-0.86	$\sigma^{18}\text{O} = 2.71 - 0.09T$
equil , 200 m, S of STC	0 m	-0.95	$\delta^{18}\text{O} = 3.28 - 0.13T$
equil , 300 m, N of STC	0 m	-0.45	$\delta^{18}\text{O} = 2.14 - 0.03T$

* Dependent variable—oxygen isotopic composition relative of PDB.

† Independent variable—average temperature at particular depths or seasons.

‡ Average $\delta^{18}\text{O}$ of shallow group (*G. ruber* + *G. sacculifer* + *O. universa*).

§ Average $\delta^{18}\text{O}$ of deep group (*G. truncatulinoides* + *G. inflata* + *G. scitula* + *G. hirsuta*).

|| $\delta^{18}\text{O}$ of equilibrium calcite at given depths or locations.

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Test ultrastructure of fusulinid Foraminifera

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Foraminifera are separated systematically at the subordinal and suprafamilial level on the basis of their wall ultrastructure¹, yet those elements of the walls are near or at the resolution of the optical microscope². To delineate those elements we have initiated a comprehensive study of the test ultrastructure of calcareous Foraminifera, utilising high voltage transmission electron microscopy (HVTEM) of specimens thinned by ion bombardment^{3,4}. We find certain ultrastructural characteristics to be common both to all Foraminifera studied and to all other comparison biological carbonate: for example, organic inclusions are found within and on the boundaries between the crystals of miliolid, fusulinid and rovaliid foraminiferal tests, bivalve shells, coral skeletons and human teeth. Other characteristics are typical of a particular host mineral, but independent of phyletic affinities: for example, the size, shape and abundance of inclusions are different in aragonite crystals from calcite crystals. Still other characteristics are diagnostic of certain groups: for example, crystal sizes and shapes are definitely different for the various suborders of Foraminifera. These ultrastructural characteristics should lead to a better understanding of the relationships between groups of Foraminifera, and to a better understanding of the biological calcification process in general. But more immediately, they provide powerful criteria for the evaluation of ultrastructural modification during and after fossilisation, especially for extinct forms such as the fusulinid Foraminifera.

Fusulinids possess one of the six major wall structure types known in calcareous Foraminifera^{1,2}. Termed microgranular, it is characteristic of all species assigned to the extinct Palaeozoic suborder Fusulinina¹. The microgranules are a few micrometres across, equidimensional and subangular². They were thought to be either agglutinated particles picked up by the organism, or as most workers now believe, to be originally secreted². As recrystallisation is common in fossils of this age, the nature of the microgranules has remained poorly understood.

These microgranules may be aligned with each other in varying degrees, thus forming fibrous or pseudofibrous layers¹. The layering arrangements in various groups of fusulinids have been well described and are used as systematic criteria¹. We are not concerned with these structures which are commonly referred to as test wall structure; we studied the internal structure of the microgranules themselves, and the relationship between them.

We consider here the ultrastructure of some well preserved specimens of *Triticites moorei* from the Wayland Shale Member of the Graham Formation (Pennsylvania) 10 miles north-east of Breckenridge, Texas (this is locality C-16 of Cushman and Waters⁵; the original description of *T. moorei* was by Dunbar and Condra⁶ from the same formation north-west of Breckenridge). From examination of numerous specimens by optical and scanning electron microscopy, we selected four for detailed study. Examination by HVTEM indicates that the specimens retain their distinctive biological ultrastructure, including preservation of minute organic inclusions.

The degree of preservation of surface morphology is excellent. In some specimens we find evidence of surface damage, perhaps due to current action before incorporation into the sediment, but no evidence of solution effects has been observed.

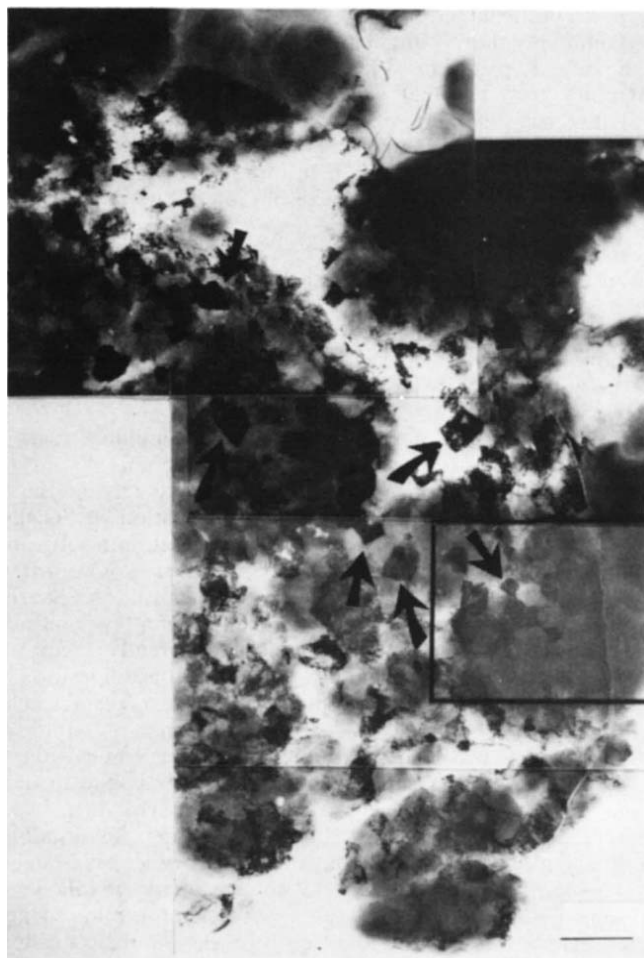


Fig. 1 HVTEM mosaic showing the general shape of test crystals and the contour of the surface. Irregular bright areas are very thin regions or holes in the specimen ($\sim 1 \mu\text{m}$ thick). Arrows point out crystals with characteristically faceted shapes. Tilting in the microscope to bring different crystals into good diffraction conditions shows that most crystals have these shapes. 1,000 kV. Rectangle shows the area of Fig. 2. Scale bar, $5 \mu\text{m}$.

By HVTEM, the lack of surface alteration is shown by the smooth outline of the test wall against the coarse 'sparry' calcite which now fills the chambers (Fig. 1). The individual microgranules of the test are equidimensional, $1\text{--}5 \mu\text{m}$ diameter crystals bounded by faces with numerous re-entrant angles (Figs 2 and 3). Note that this microstructure is distinctly different from that produced by recrystallisation of calcite or other monomineralic substances (for example, photomicrographs and electronmicrographs of recrystallised calcite, quartz and olivine are indistinguishable from each other⁷⁻⁹). A recrystallised microstructure consists of equant crystals with dominantly planar faces such that the grain boundaries approximate a 'foam' structure produced by equilibration of grain boundary energies. Re-entrant angles are exceedingly rare, and the orientation of crystal faces is unrelated to the crystallography of individual crystals. In these fusulinids, however, the opposite is true; re-entrant angles are common (Figs 2 and 3) and large numbers of crystals have symmetrically related faces (Figs 1 and 2) and faces parallel to internal surfaces (Fig. 3). These features are reminiscent of the miliolid wall structure seen in HVTEM of *Alveolina quoyi* d'Orbigny, although in the miliolids the crystals are greatly elongated in one direction (compare with Pl. 9, Fig. 4 of ref. 4). Within the fusulinid crystals and on the boundaries between them, voids are abundant (Fig. 3). These voids range downward in size from $\sim 1,000 \text{ \AA}$ to $< 50 \text{ \AA}$. Within individual crystals, voids tend to be approximately spherical or ellipsoidal,

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but some of the larger ones are irregular. Grain boundary voids are commonly sharply angular and frequently a tetrahedral gap with perfectly planar faces left between four crystals which did not quite grow together can be seen (Fig. 3c). These voids probably contained organic matter originally, but are now empty. In addition to the voids, however, all crystals of the test contain myriads of very small inclusions with images ranging in size from ~ 100 Å down to the resolution of the microscope, ≈ 4 Å (Fig. 3b). The visibility and apparent size of these inclusions are critically dependent on the diffraction conditions because they produce strain contrast in the host calcite; hence their maximum size may be < 100 Å. The inclusions are concentrated on low angle (subgrain) boundaries but are also abundant in regions of perfect crystal. Dislocations are rare in these crystals; some do and others do not have concentrations of inclusions along them.

In contrast to the crystals of the test, the infilling 'sparry' calcite crystals are very coarse-grained, and commonly only a few crystals fill an entire chamber. Voids are rare in these crystals and inclusions are totally absent. Dislocations are locally abundant (Fig. 2) and are occasionally organised into subgrain boundaries; in other areas the dislocation density is very low ($< 10^6 \text{ cm}^{-2}$). In many areas the infilling calcite displays a poorly defined lamellar structure with a wavelength of a few hundred ångströms (arrow, Fig. 2). This latter structure greatly resembles the incipient exsolution lamellae (spinodal decomposition?) common in pyroxenes from igneous rocks¹⁰ and may represent a similar phenomenon.

Alteration of fossils by solution effects or recrystallisation is very common¹¹. As a consequence we initially hoped to find some small regions of the samples which might have been preserved through the nearly 300 Myr since their fossilisation. Surprisingly, we find that virtually everything we see seems to be free of modification. We reach this conclusion by the following reasoning: (1) Even on the scale of the electron microscope, external form of the fossils is faithfully preserved; the transition to the infilling calcite is abrupt. (2) The crystal shapes are unlike any polycrystalline calcite ever described; in particular they are unlike extremely fine-grained natural and experimentally recrystallised material⁹. Moreover, except for lack of elongation, these crystals and the voids between them display many of the characteristics of living miliolids⁴; the shapes observed seem to be the result of mutual interference of faceted crystals

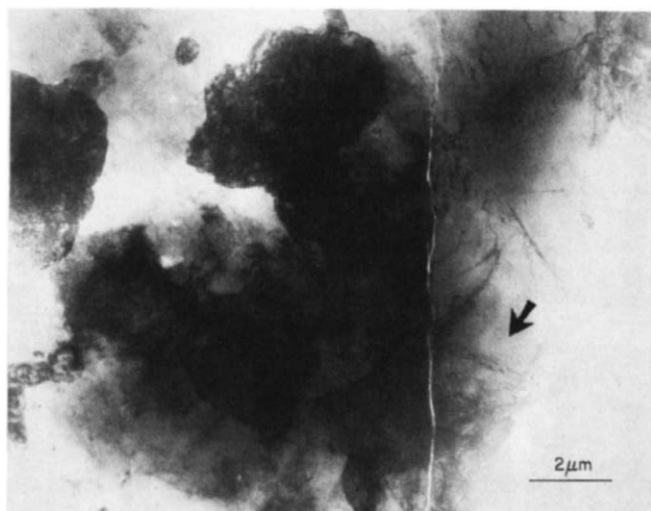


Fig. 2 Detail of portion of Fig. 1 with specimen tilted to a new orientation to show clearly the substructure of the infilling calcite. Note that the crystals of the test appear different than in Fig. 1. This is due to change in the diffraction conditions of individual crystals. Arrow points to lamellar feature in infilling calcite (see text). Scale bar, 2 μm .

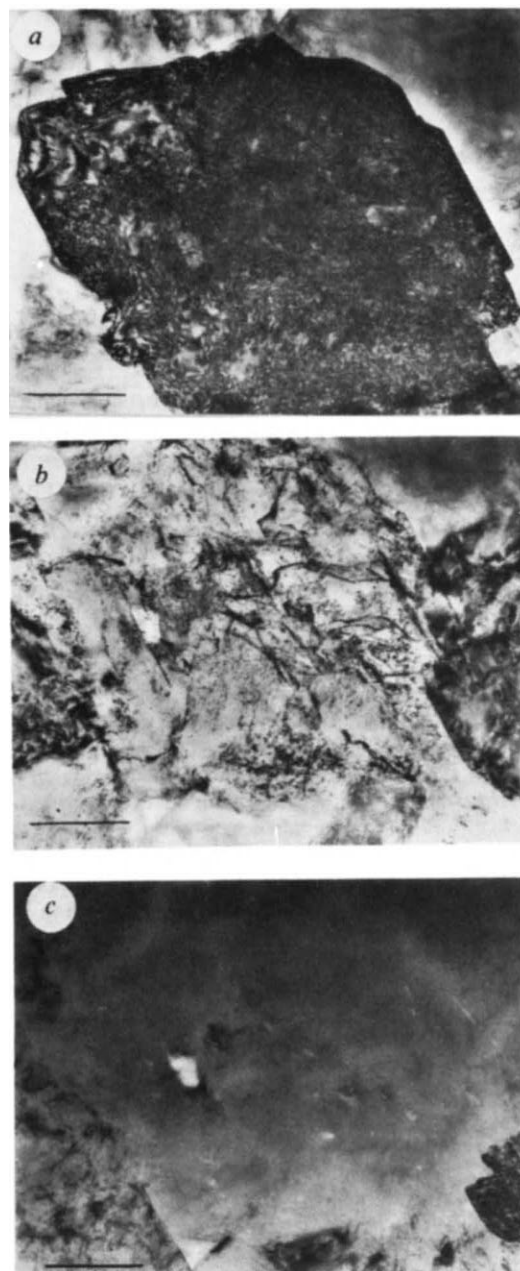


Fig. 3 Detail of typical crystal from interior of test wall. Note planar crystal faces with re-entrant angles. 1,000 kV. Scale bars, 1 μm . *a*, Crystal in strong diffraction contrast. Irregular mottling is caused by elastic distortion of crystal around minute inclusions. *b*, Same crystal, different tilt. Crystal now is in strong contrast only in distorted regions around inclusions. Note internal boundaries parallel to external faces. *c*, Same crystal, tilted to minimise contrast around inclusions. Numerous voids are now visible, including the large triangular one at the lower left where a corner of this crystal meets two others. Note that in detail this void is a triangular pyramid with planar sides.

growing in an isotropic medium—like crystals in an igneous rock. (3) The pattern of voids and minute inclusions in the crystals of the test is distinctly different from that of the infilling calcite, yet absolutely characteristic of the shells of Foraminifera and other organisms^{3,4}. (4) The infilling calcite contains a lamellar structure which is not found in the tests, suggesting a different chemistry.

Of course, a pseudomorphous replacement of the original crystals (calcite or another mineral) could be postulated such

that the original, biogenic texture was preserved. This is unlikely because no evidence of such replacement has been found. Moreover, the distribution of inclusions makes such an *ad hoc* hypothesis doubtful because the behaviour of both fluid and solid inclusions during inorganic recrystallisation is well known: inclusions either interfere strongly with grain growth, resulting in a distinct and characteristic modification of the texture, or they are swept out of the interior of grains and concentrated at the boundaries. We do not know of any case where large numbers of very small inclusions remain undisturbed as a grain boundary migrates past them, nor would it be expected.

The similarities to miliolid ultrastructure and the similarity of both to interference structures such as in igneous rocks or metal castings suggest that the individual crystals grew independently in a fluid or fluid-like environment (in this case probably organic matter)². Each crystal grew with its characteristic crystal faces until it came into contact with other crystals. At the point of contact the two crystals would interfere and one or both would lose its crystallographically controlled shape. The preservation of part or all of the crystal form on the majority of crystals indicates that, as in the miliolids, the calcification process did not go to completion; a significant volume remained occupied by organic matter. This is also likely to be the process of calcification of miliolids; it is possible that the different crystal shapes between the two groups are controlled by the chemistry of the organic medium, much as experimental crystal growth can be controlled by adsorption of specific impurities on certain crystal planes.

Although we argue that the basic microgranular test ultrastructure is original, two types of alteration could still be present: (1) Part of the original intercrystalline organic matter may have been replaced by inorganic calcite during diagenesis. We believe that any such replacement must have been minor because there is no general fine-grained matrix between original crystals, and the pattern of inclusions within the original crystals extends to the grain boundaries, making diagenetic overgrowths also unlikely. (2) The chemistry of the test calcite crystals could conceivably have been modified. Towe and Hemleben¹¹ have shown that fossil miliolids can retain the external form of their original crystals, yet have a much lower Mg content than the crystals of living miliolids. It remains to be demonstrated whether such cation exchange could leave unaltered the pattern of minute inclusions within crystals reported here.

The strong strain contrast around the intracrystalline inclusions indicates that they remain filled. The same effect is apparently seen here as that around the inclusions in living species of Foraminifera and other organisms, and in these latter cases the larger inclusions can be seen to contain organic matter⁴. Unfortunately, we have not found any inclusions in these fusulinids which are large enough to identify organic matter positively within them (the same is true for many modern foraminiferal tests; those that have very small crystal sizes also have very small inclusions). Nevertheless, the evidence suggests that the original contents of these inclusions are still there—locked away and protected inside their calcite ‘bottles’—and possibly material could be concentrated from specimens and analysed.

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Genetic heterozygosity in a natural population of *Mus musculus* assessed using two-dimensional electrophoresis

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Since the introduction of gel electrophoresis to population genetics, estimates of genic heterozygosity at allozyme loci have been made for many organisms¹. However, attempts to extend the range of proteins surveyed²⁻⁴ have been hampered by concern that there may have been bias in the loci sampled: nearly all proteins for which population data are available are soluble in low-salt extracts and most are enzymes belonging to particular groups such as the nonspecific esterases and phosphatases, various dehydrogenases and the enzymes of the glycolytic pathways and the citric acid cycle. Until recently, there were no techniques for estimating protein variation which were without such bias. Two-dimensional gel electrophoresis⁵, however, offered hope of overcoming this bias, and it has proved useful for the resolution of proteins in crude homogenates and for estimating genetic variation⁶⁻⁹. We have examined heterozygosity in a wild population of the house mouse (*Mus musculus*) by means of two-dimensional electrophoresis of whole kidney. As we report here, the observed level (2%) is substantially below the level detected by starch gel electrophoresis¹⁰⁻¹². Our results corroborate similar differences observed in *Drosophila*⁶ and man^{7,9}.

The O'Farrell⁵ technique is a method for high-resolution, two-dimensional separation of proteins in polyacrylamide gels. It involves two independent criteria for separation. In the first dimension, denatured proteins are separated according to their molecular weight as assessed by SDS electrophoresis. However, certain questions must be answered before the method can be applied to surveys of genetic variability. Can products of distinct structural loci be distinguished? Can allelic substitutions at a single locus be distinguished? What is the bias of this method with respect to the protein type examined? From O'Farrell's⁵ original estimates and from subsequent experiments¹³, it is evident that gene products of different loci can routinely be distinguished, and that amino acid substitutions involving residues of different charge will be detected^{14,15}. However, there seem to be other, perhaps conformational, differences^{6,16} detectable by native electrophoresis (electrophoresis in non-denaturing conditions), or native isoelectric focusing (IEF) that are not detected with O'Farrell's technique. The inherent bias of this technique is towards loci with more abundant gene products, as the detection depends on nonspecific protein staining or labelling.

Figure 1 shows a typical two-dimensional protein pattern from a SDS-urea extract of a mouse kidney. About 100 spots can easily be scored. In our survey, we scored only spots in the

Table 1 Polymorphic loci detected in the Skokholm wild population of the house mouse (*Mus musculus*)

Allele designation	Frequency	Expected heterozygosity
a_1	0.64	0.46
a_2	0.36	
h_1	0.44	0.49
h_2	0.56	
i_1	0.80	0.32
i_2	0.20	

Expected heterozygosity is calculated as $1 - (f_1^2 + f_2^2)$, where f_1 and f_2 are the frequencies of the number 1 and 2 alleles, respectively.

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central region of the gel, as the pH gradient (indicated in Fig. 1) becomes nonlinear at the edges, resulting in loss of resolution in the IEF. We identified three spots showing variation consistent with a simple genetic interpretation¹⁷ (Fig. 2). Protein *a* is isocitrate dehydrogenase (Id-1), which maps on chromosome 1 (ref. 17). The frequencies of the alleles controlling the variant Id-1 spots are shown in Table 1. We were not able to identify the biochemical role of the other two proteins¹⁷. Table 2 summarises our results and gives the calculated average per-locus heterozygosity together with information on the allozymic variation provided by Berry¹⁰.

We have taken into consideration the fact that a single allele of locus *a* (identified as Id-1) displays two spots on a two-dimensional gel by doubling the expected heterozygosity of locus *a* (Table 1) for calculating our average per-locus heterozygosity. The display of two spots by one allele is probably a result of the long storage time of the kidney tissues (>2 yr, R. J.

Berry, personal communication), as we did not observe this on fresh samples¹⁷. In connection with another study¹⁷, we have made a similar observation with 2-yr-old purified Id-1 enzyme¹⁸. This enzyme preparation displayed several spots across the slab gel at the appropriate molecular weight (R.R.R., C.H.L. and C.-Y. Lee, unpublished results). Similar multiple spots per allele have been reported^{9,14}. The 17 loci known to show genetic variation in these studies exhibit 20 spots on two-dimensional gels^{6,9,14,17}. We can therefore estimate that the number of loci surveyed is 85% (17/20) of the number of spots scored. The number of consistently scorable spots (85) probably then represent about 72 individual structural loci.

The threefold reduction in heterozygosity (Table 2) obtained by two-dimensional rather than native electrophoresis on the same mice is striking. This observation is in accordance with studies on *Drosophila*⁶ and man^{7,9}. The difference probably arises from the ability of two-dimensional gel electrophoresis to

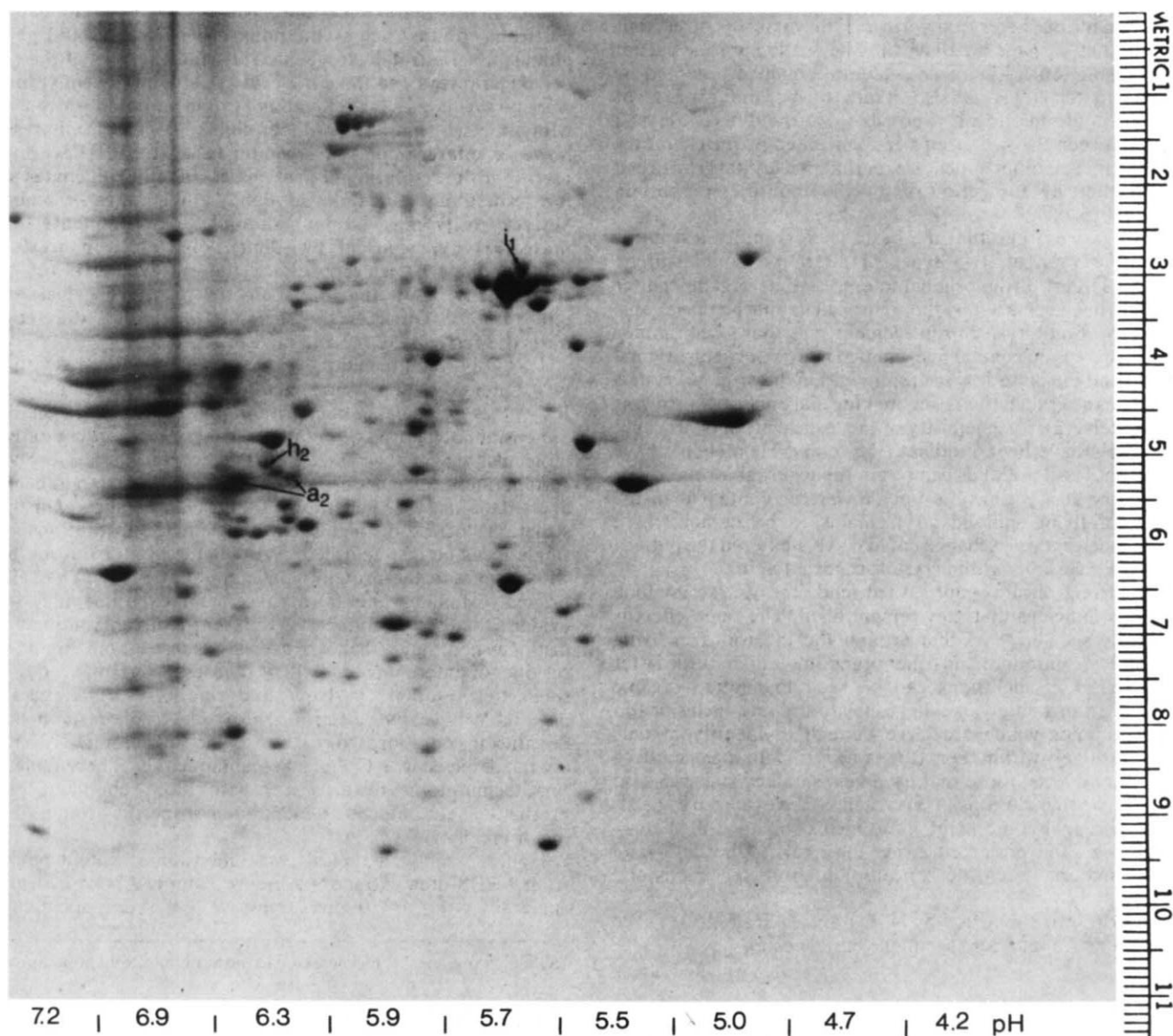
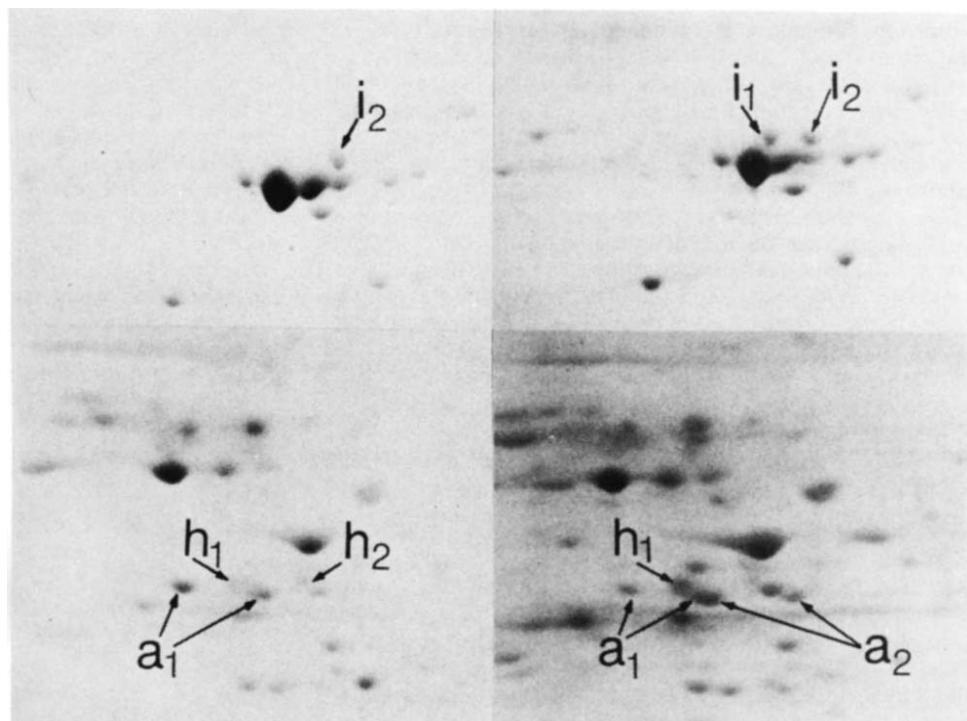


Fig. 1 Two-dimensional gel of a crude kidney homogenate of a wild mouse from Skokholm. *a*, *h* and *i* refer to the three polymorphic spots found. Samples were prepared according to the method described by Wilson *et al.*²⁰. Samples (50 μ l) were loaded onto the isoelectric focusing (IEF) gels following the procedure of O'Farrell⁵. IEF was carried out in 11.5-cm long Pyrex tubes with an internal diameter of 2 mm, using the same mixture of pH 3.5–10 and pH 5–8 carrier ampholytes as O'Farrell. SDS slab gel electrophoresis in 10% acrylamide was also carried out as described by O'Farrell. All slab gels were fixed in a mixture of 45% methanol and 10% acetic acid overnight and stained in the same solution containing 0.02% Coomassie brilliant blue R-250. Gels were destained in a mixture of 25% methanol and 7% acetic acid. They were photographed on Polaroid type 55 positive/negative film with a red filter. Throughout, 1% dithiothreitol (Eastman) was used instead of 5% mercaptoethanol. All other reagents were obtained from the same sources⁵. Molecular weights in the slab gels were determined by running in parallel RNase (13,000), chymotrypsinogen (25,000), aldolase (subunit 40,000) and ovalbumin (45,000) (all Pharmacia).

Fig. 2 Two-dimensional gel patterns of the variant regions.



survey previously inaccessible classes of proteins. The two techniques cannot be directly compared, as IEF is not capable of resolving several enzyme variants in *Drosophila* which can be distinguished with standard, one-dimensional methods¹⁶. Leigh Brown and Langley⁶ have compared 10 species of *Drosophila* using α -glycerophosphate dehydrogenase identified on a two-dimensional gel. Several species showed slight differences in mobility in standard starch gel conditions, but on two-dimensional gels only major charge differences (such as the usual slow/fast polymorphism) were detected. Carbamylation experiments^{14,15,19}, however, show that two-dimensional electrophoresis can resolve all substitutions in the primary structure of a protein which result in a charge difference. The extra variation observed in native, one-dimensional gels is therefore either conformational or post-translational in nature. As the two-dimensional gel technique detects only charge-change substitutions, estimates of total heterozygosity are impossible.

Table 2 Comparison of average per-locus heterozygosity levels between two-dimensional (2-D) and starch gel electrophoresis evaluated in the same wild mice from Skokholm

	2-D gels	Starch gels
No. of loci scored	72 (85)	26
No. of loci polymorphic	3	5
Expected heterozygosity	0.020*	0.172

Number in parentheses indicates the actual number of proteins scored. For further explanations see text. Starch gel data are from an extensive study done by Berry¹⁰.

* Calculated $0.020 = (2 \times 0.46 + 0.49 + 0.32)/85$.

However, if the conditions used in most standard, one-dimensional surveys of allozyme variation are also such as to detect only full charge differences, as is likely, the drop in heterozygosity evaluated by two-dimensional electrophoresis compared with standard electrophoresis, is striking. It might suggest that the most abundant proteins in mouse kidneys represent a group of proteins which are different from and less variable than those which are detected in standard electrophoresis. However, if the proteins identified with the two-dimensional technique are representative of most mouse proteins, the average level of genic heterozygosity is much lower than that previously estimated.

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Identification of specific leech neurones immunoreactive to enkephalin

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The small endogenous peptides, Met- and Leu-enkephalin, bind to the same specific receptors as opiate analgesics. They, and the larger endorphin peptides, have been widely found in mammals, where they seem to have a significant role in neuronal pathways mediating pain and emotional behaviour. Only recently has enkephalin-like activity been identified in an invertebrate, the earthworm¹, although there is some preliminary evidence for opiate receptors in a marine mollusc². Here I report the detection, by an immunocytochemical technique, of an enkephalin-like moiety which is localised in one of the 400 cells of each posterior midbody ganglion of the leech. The presence of enkephalin-like activity in an identifiable easily accessible neurone of a well characterised nervous system such as that of the leech³⁻⁵ could greatly facilitate elucidation of its mechanism of action.

Neurones in the refrigerator-stored leech react optimally to Leu-enkephalin antisera (Immuno Nuclear Corporation) at dilutions of 1/5,000 and 1/10,000. The same concentrations of this batch of serum also gave optimal immunocytochemical staining of monkey spinal cord sections (Ellyn Glazer, personal communication), indicating that the immunoreactivity to enkephalin in leech ganglia is of similar strength to that in the mammalian material.

Figure 1a shows a series of three successive midbody ganglia from a single leech stained for Leu-enkephalin. Only one cell body at about the same position in each ganglion is immunoreactive. This 30- μm cell body appears on the ventral surface in the posterior half of the ganglion. A stained process leading from this cell body can occasionally be seen in the microscope but is hardly visible in the photographs.

500, 100 and 20 $\mu\text{g ml}^{-1}$. The 30- μm cell body was not stained over this full 25-fold range. The reaction of the varicosities was concentration dependent; they were not stained when the serum was blocked with Leu-enkephalin at 500 and 100 $\mu\text{g ml}^{-1}$, but reappeared faintly at 20 $\mu\text{g ml}^{-1}$.

In ganglia 5, 6 and 7, instead of a single neurone, several cell bodies can show immunoreactive product. Ganglia 5 and 6 innervate the sex organs and are about 80% larger than the typical midbody ganglion; ganglion 7 has no known specific function.

The most significant aspect of this work is that antisera to Leu-enkephalin reacts positively with one specific cell body that maintains the same size and location in successive ganglia within the posterior two-thirds of the midbody ganglionic chain. By analogy with other leech neurones, it is likely that these cell

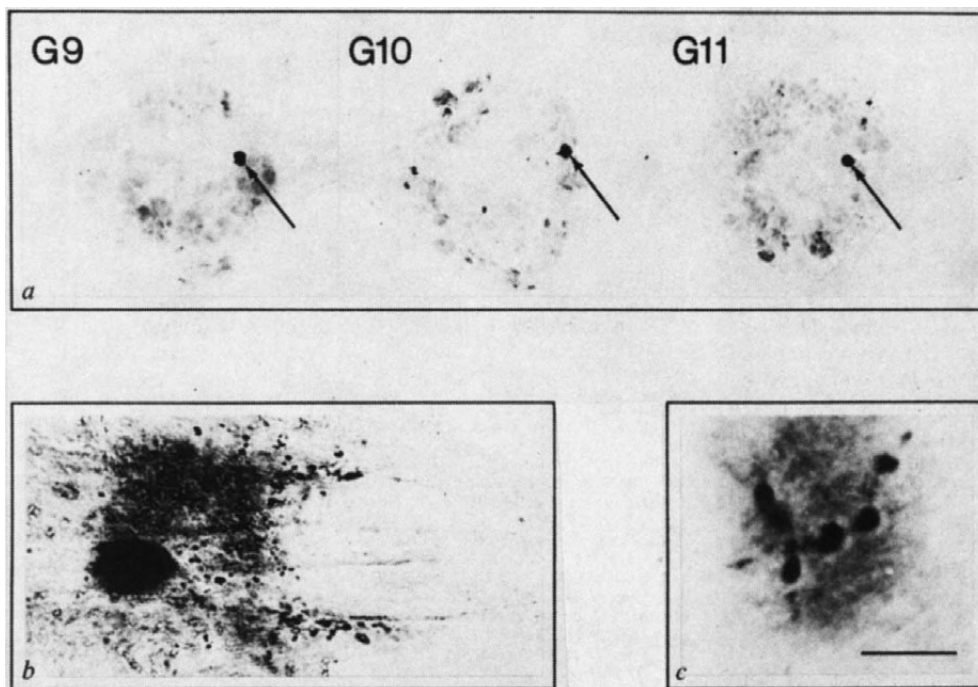


Fig. 1 Enkephalin-immunoreactive cell bodies and neuritic processes in leech ganglia. *a*, A specific cell body in successive ganglia of a *Haemaphys marmorata* leech stained by reaction with PAP-coupled Leu-enkephalin antisera. *b*, *c*, The central neuropile showing immunoreactive processes and varicosities. The immunocytochemistry was done on whole ganglia whose ventral capsules were cut to expose the ventrally located unipolar cell bodies. To facilitate diffusion of antibodies across membranes, the 4% paraformaldehyde-fixed ganglia were put through a successive alcohol series into xylene and brought back into buffer before a 2-day incubation with serum containing 0.2% saponin. Calibration: *a*, *b* and *c* are 150, 35 and 13 μm , respectively.

Figure 1b and c show photomicrographs of the central neuropile of a midbody ganglion at two magnifications. In Fig. 1b, a pattern of immunoreactive varicosities is visible. These darkly staining entities at the level of the neuropile strongly resemble nerve terminals of other neurones in the leech⁶. They seem to have a wide size range, with the largest reaching about 4 μm . The individual varicosities are visible at the high magnification of Fig. 1c. These varicosities are present in all ganglia, even those in the anterior cord, where cell bodies are generally not stained.

The presence of bound antibody was demonstrated using the peroxidase-antiperoxidase (PAP) procedure developed by Sternberger⁷. Following the incubation with rabbit anti-Leu-enkephalin (Immuno Nuclear Corporation), the ganglia were washed and incubated with goat anti-rabbit IgG (1/20; Cappel) for 30 min, then with the PAP complex (1/250; Cappel) for another 30 min, and finally stained by reaction of peroxidase with 3',3'-diaminobenzidine.

Non-immune and Leu-enkephalin-blocked controls were run to confirm that the stained structures were reacting specifically to antibodies against enkephalin. Half ganglionic chains of three different leeches were incubated with non-immune serum of the same dilutions as the enkephalin antisera and neither the 30- μm cell body nor the varicosities were stained, whereas material from the same leeches run in parallel with enkephalin antisera was stained. Leu-enkephalin antiserum was blocked by incubation with Leu⁵-enkephalin (Boehringer) at concentrations of

bodies are homologues which can be identified and studied electrophysiologically. It will be interesting to see if the pattern of enkephalin-like distribution observed here with leeches kept in the cold changes when animals in different behavioural states are studied.

The varicosities that show up so prominently with Leu-enkephalin antisera are presumably enlarged synaptic endings with a high peptide content, as they reappeared earlier than the cell bodies when the enkephalin concentration blocking the antiserum was lowered to 20 $\mu\text{g ml}^{-1}$. Near the head there are ganglia with clearly stained varicosities but no stained cell body, indicating either that not all enkephalin-containing neurones have stained cell bodies, or that some enkephalin-containing terminals originate from cells in other ganglia.

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Reversible events in the transduction process of photoreceptors

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In photoreceptors, a latency of many milliseconds elapses between the absorption of a light quantum and the occurrence of the late receptor potential, even for strong light stimuli. Surprisingly, this is much longer than the time necessary for conductance changes such as occur in membranes of neurones or muscles, mediated by chemical transmitters. There are several possible explanations for the long photoreceptor latency. (1) It may be due to properties of the visual pigment molecules. For instance, the temporal coincidence of the occurrence of meta-rhodopsin II with the receptor signal indicates that the meta I-meta II transition might be the trigger for the electrical response in vertebrate photoreception¹. (2) It may be explained by properties of transport processes. Such a time consuming process could be the diffusion of an internal 'transmitter substance', which diffuses to a 'pore' in the receptor membrane. (3) A third possibility is the time needed to produce and accumulate chemical substances. The light-induced change of the visual pigment molecule might trigger a chemical reaction chain, in which the product of an earlier step triggers the next one. The experiments described here show that a considerable part of the long latency in photoreception is due to processes that are localised at the level of the visual pigment molecule.

Photoreceptors of invertebrates have a stable metarhodopsin (M), which is reconverted into rhodopsin (P) by absorption of light^{2,3}. This 'bi-stability' offers the possibility of discriminating between the different hypotheses. In the photoreceptors called R₁₋₆ of the fly compound eye the transition of rhodopsin (P) into metarhodopsin (M) is fast (time constant $\approx 100 \mu\text{s}$ at room temperature, $500 \mu\text{s}$ at 10°C)⁴. This excludes the possibility that the kinetics of the photometrically determined pigment transition is the time-limiting process. Hypothesis (1) can thus be valid only if properties of the photopigment molecule other than those detectable photometrically are involved. The bi-stability of the visual pigment system of the fly photoreceptors allows one to reconvert $M \rightarrow P$ within the latency of the response. If hypotheses (2) or (3) were correct, an irreversible process should have been initiated within a fraction of a millisecond, and the reversion of $M \rightarrow P$ should not affect the response. These hypotheses therefore can be rejected if it can be demonstrated that the reversion reduces the response.

As will be seen below, a successful experiment can be performed only in receptors in which the rhodopsin content has been reduced to low concentration.

Figures 1 and 2 show the amplitude of the receptor response to light flashes as a function of intensity. With strong stimuli the response amplitude becomes saturated.

In the visual pigment system of receptors R₁₋₆ of the blowfly, blue light shifts a maximal fraction of P into M, red light a maximal fraction of M into P^{5,6}. With short double flashes (blue followed by red), P can be first converted to M and then back again within the latency of the response. The effect of such double flashes on the prolonged depolarising after-potential and the 'pupil response' in *Calliphora* has been described by Muijser and Stavenga⁷.

Figure 1c shows responses to a blue flash and to the sequence blue-red. It is obvious that, compared with the single blue flash, the second red flash reduces the response amplitude. This result seems to be paradoxical because more absorbed light quanta

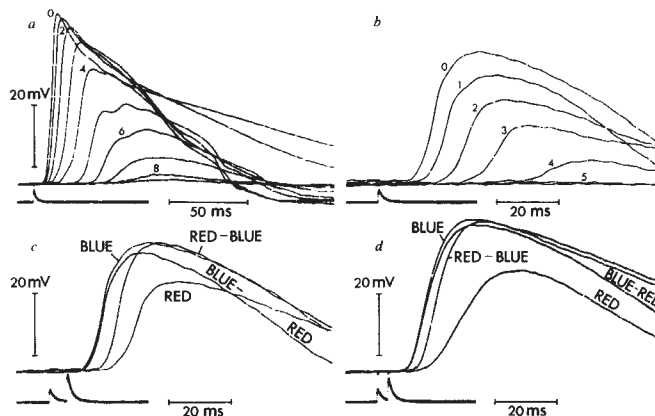


Fig. 1 Intracellularly recorded responses of photoreceptors (type R₁₋₆) of *Calliphora* female, chalky, to light flashes. Monitor, lower trace; temperature, 10°C . *a*, Fly with high rhodopsin content in the receptors. Relative flash intensities were changed from 10^0 to 10^{-9} (numbers indicated on the traces). *b*, Fly with rhodopsin content reduced to 1/1,000 of normal. *c*, Same cell as that used in *b*. Stimulus, blue and red single flashes; blue-red and red-blue double flashes with 5 ms delay, all of maximal intensity. Note that the longer latency of the sequence red-blue is due to the fact that the blue flash occurs as the second one. *d*, Same stimulus programme as used in *c*, delay between double flashes 3 ms; records from another fly.

lead to a smaller response. This paradoxical result is obtained only with the sequence blue-red, whereas the sequence red-blue leads to the same response amplitude as a single blue flash. Blue-blue double flashes always result in an increase of the response amplitude as long as the response has not been saturated by the first flash, and if the second flash is not given too late.

The amplitude to the sequence blue-red corresponds to an amplitude to a single blue flash reduced to some 25% of maximal intensity. This can be seen from the intensity amplitude function (Fig. 2). The response is not completely abolished for two reasons. First, for technical reasons, the second red flash was not bright enough to reach equilibrium completely. Hence, from the M created by the first flash, only two-thirds are shifted back into rhodopsin. Second, the red flash by itself shifts a small amount of P into M. From the amplitude of the red response this amount can be estimated to be 1-2% (see arrow in Fig. 2).

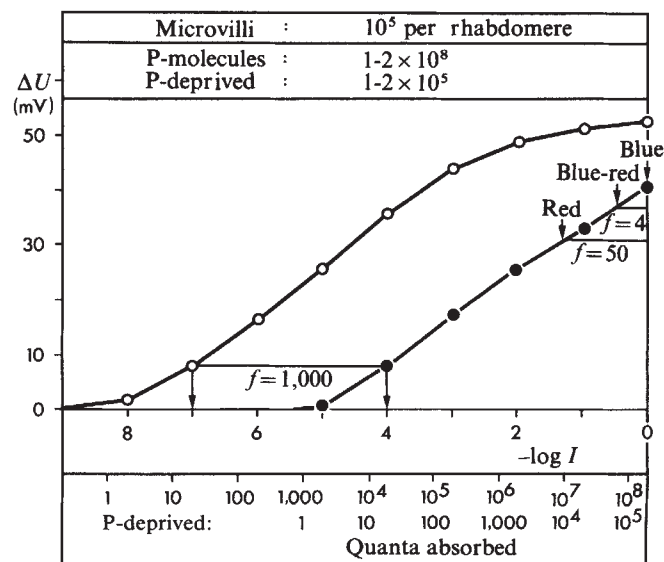


Fig. 2 Amplitude-response functions of a receptor of high (○) (Fig. 1a) and low (●) (Fig. 1b) rhodopsin content, respectively. Abscissae, $-\log$ relative intensity; quanta absorbed. Ordinate, amplitude of receptor potential in mV. Arrows indicate amplitudes of responses from Fig. 1c to blue, blue-red and red flashes. *f* values indicate sensitivity factors.

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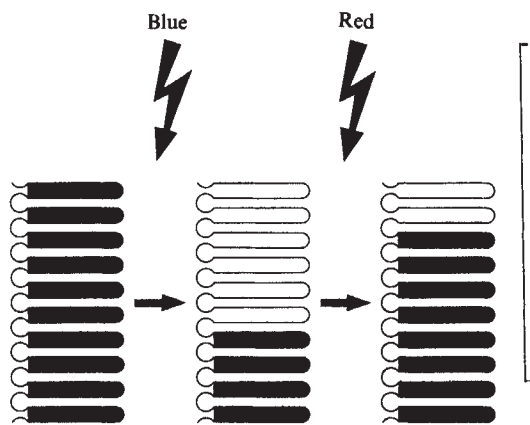


Fig. 3 Microvilli (shown schematically) with visual pigment in either rhodopsin (P) (black) or metarhodopsin (M) conformation. The first blue flash shifts some 60% of P into M; after the second red flash only 20% of the pigment is left as M.

If we want to stop the conductance change induced by the P→M conversion, we must hit the same molecules with the second red flash. The probability of doing so is high only at very high flash intensities which already saturate the cell. Hence, a possible reduction of the response to the blue–red double flash cannot be detected at normal visual pigment content of the receptors. To remain below the saturation of the response we must reduce the pigment content to such a degree that less than 10^5 pigment molecules can be hit; this means that the pigment concentration must be $<1\%$ of normal⁸. (The reduction in P content to $<1\%$ of normal was achieved by raising flies in special conditions developed by Schwemer⁹.) In this condition, the sensitivity of the receptors is markedly reduced (Fig. 2), but, as has been shown, the double-flash experiment can be successfully performed (Fig. 1c, d). Quantitatively we obtain the following situation. The first blue flash shifts 60% P into M. The second red flash shifts back 65% of those M molecules, so that 20% remain (Fig. 3). These values have been derived from photometrical measurements in the experimental set-up used for the electrophysiological experiments¹⁰.

If the pigment content is sufficiently reduced, the amplitude to the blue–red double flash is always smaller than that to the blue flash alone. However, the amplitude reduction was often not as prominent as that shown in Fig. 1c, and corresponded to a loss in sensitivity by a factor of only 2 to 3.

Following the conversion of P to M ($\tau \approx 500 \mu\text{s}$, 10°C), there remains a period of 3–5 ms during which reversion of M to P more or less completely abolishes the effect of the initial P→M conversion (Fig. 1c, d). During this period no irreversible transmitter release or chain reaction could have been initiated. It is true that there remain a further 3–4 ms before the onset of the response during which such processes may become important. What has been clearly shown is the existence of a distinct, time-limiting process in transduction localised at the level of the pigment molecule and lasting a few milliseconds.

Furthermore, we are able to decide whether the response of the receptor is due to the total number of P→M conversion or to the number of M molecules remaining after the stimulus. Because, in both flash sequences (red–blue; blue–red), the number of P→M conversions is the same whereas the number of M molecules remaining is different, it must be the M molecules remaining after the flashes which trigger the conductance change.

As we are able to stop the sequence of events within 3–5 ms, the action of the freshly created M must last longer than 3–5 ms in order to trigger the response. After having excited the membrane, the M molecules remain as thermostable M without any further excitatory effect. Therefore, it is the newly created M which excites the membrane. This M has been called 'energy rich' in the photoreceptor membrane model developed from other experimental evidence¹¹.

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Photoreceptor signals at visual threshold

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Electrical responses of cone photoreceptors in the retina of the freshwater turtle have been characterised for flashes and steps of light in darkness and in the presence of background light^{1–4}. These intracellular measurements have been combined with the behavioural increment threshold curve to yield an estimate of 5–10 μV for the signal developed in a cone when the turtle can just detect an increment flash⁵. The signal developed when the cones under the stimulus image are dark-adapted is of interest, for its measurement would help to explain how known physiological processes subserve visual detection for a variety of photic conditions. The effective quantal absorption of dark-adapted, red-sensitive cones of *Pseudemys scripta elegans* for a stimulus that the turtle can just detect is reported here. By combining this result with previous electrical measurements on red-sensitive cones of this species, an estimate of 35–70 μV is obtained for the signal developed in a dark-adapted cone at behavioural threshold. This larger signal required for detection of a flash in darkness is of particular interest in view of the recent observation⁶ that the intrinsic noise of turtle cones in darkness is larger than that of illuminated cones.

Details of the experimental apparatus and the behavioural paradigm have been presented elsewhere^{1,7}. Basically, the animal was placed in an experimental chamber with its head positioned so that the stimulus image fell on the central linear streak of the retina. The turtle was trained to avoid an electric shock by pulling in its head whenever it detected a flash of light. An 'up-down' tracking procedure was used to determine the threshold with mean 95% confidence intervals of about 0.1 log units. The animal was dark-adapted for 45 min before presentation of a 2.35° diameter stimulus for 125 ms. As these values represent the approximate critical area and the exact critical duration for white (tungsten) light (see Figs 31 and 32 in ref. 1), essentially complete spatial and temporal summation occurred. The radiant emittance M_e of the source was determined as a function of wavelength using a calibrated thermopile, and for the attenuated stimulus was $2.1 \times 10^{-8} \text{ J cm}^{-2} \text{ s}^{-1}$. From Lambert's law the radiance L_e of the stimulus was $6.5 \times 10^{-9} \text{ J cm}^{-2} \text{ sr}^{-1} \text{ s}^{-1}$. The retinal irradiance E_e can be determined⁸ from the relation $E_e = \pi L_e (n.a.)^2$ for a numerical aperture (n.a.) that is equal to $nd/2p$ for refractive index n , entrance pupil diameter d and posterior focal length p . We used values of $n = 1.34$ and $p = 6.40 \text{ mm}$ from the schematic eye of *Pseudemys*, which has an actual pupil diameter of 1.74 mm (data of D. P. M.

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Northmore in ref. 1). The entrance pupil is located 0.21 mm anterior to the actual pupil, and was determined to be 1.95 mm in diameter using the corneal magnification factor, which was calculated to be 1.12. This agrees fairly well with the approximate 10% reduction of apparent pupil size when the animal is placed in water, thereby cancelling the refractive power of the cornea. The resultant numerical aperture is 0.203, which, when substituted into the relation for the attenuated retinal irradiance, yields $8.6 \times 10^{-18} \text{ J } \mu\text{m}^{-2} \text{ s}^{-1}$. When the neutral density of the optical media (0.04) (ref. 9) is taken into account, this figure is reduced to $7.9 \times 10^{-18} \text{ J } \mu\text{m}^{-2} \text{ s}^{-1}$. The fraction of this just-detectable light at the level of the retina that is effective in terms of the red-sensitive cones was determined by numerically integrating the product of the mean spectral sensitivity of the cones and the spectral distribution of the light, then dividing by the integrated spectral energy of the light. The resulting value is 0.52. This reduces the retinal irradiance to $4.1 \times 10^{-18} \text{ J } \mu\text{m}^{-2} \text{ s}^{-1}$, which represents the total energy in the stimulus to which red-sensitive cones are sensitive irrespective of wavelength. The optimal wavelength for both the cone sensitivity² and the light spectrum is 633 nm, and by weighting the energy at this wavelength a conversion to quanta can be made with a result of 1.6 quanta μm^{-2} per flash. The mean cross-sectional area of a 3.0- μm diameter oil droplet in a paracentral, red-sensitive cone of *Pseudemys*¹⁰ is $7.1 \mu\text{m}^2$, yielding an average of 11.4 quanta per cone per flash based on the area of the oil droplet. This value is an estimate of the minimum quantal catch by the cone, as oil droplet area is on the average only half the area of the inner segment, according to measurements made prior to the droplet in peripheral cones¹¹. Thus, if twice as much light were collected by the cone in view of this possible twofold difference, this value could be as high as 22.8 quanta per cone per flash. Approximately 12% of these 11.4–22.8 mean incident quanta are effectively collected, absorbed and transduced by the outer segment of a red-sensitive cone¹¹, so on the average 1.4–2.8 quanta are effectively used by each red-sensitive cone at the behavioural threshold. Since each effective photo-isomerisation in a peripheral red-sensitive turtle cone yields a hyperpolarisation of the membrane potential of about 25 μV (ref. 2), an average signal of between 35 and 70 μV is developed in each red-sensitive cone in response to a flash of light that the dark-adapted animal can just detect. An assumption made in arriving at this range is that paracentral, red-sensitive cones also develop approximately 25 μV per effective photo-isomerisation when a large number of adjacent cones are illuminated, as was the case in the determination of the response of peripheral cones.

For the data used in this analysis the results provide an estimate of what is probably a minimum range of effectively utilised quanta: the most sensitive electrophysiological and behavioural data available have been incorporated in our calculations. The use of any other data, such as larger red-sensitive cone diameters for measurements^{10,11} taken from the peripheral retina of *Pseudemys*, would yield a larger estimate. To assure that no substantial error was introduced due to the use of white (tungsten) light, we also determined thresholds for red light by inserting a colour filter (Kodak no. 26) in the light path. Because of the decrease in total light available to the red-sensitive cones, the neutral density had to be decreased by 0.15 units in order to obtain an equivalent threshold. Of the red light thus presented we calculated that a difference of about 0.14 log units existed between the two stimuli in terms of their effectiveness in stimulating red-sensitive cones, in comparison to the 0.15 units found experimentally. Similar thresholds for the two stimuli are actually expected in view of the long-wavelength spectral bias of both the animal's sensitivity and the energy of either stimulus. Within experimental error (0.01 density unit), then, we have a determination of threshold using red and white lights that strongly suggests that the animal is using its red-sensitive cones to detect the spectral energy of both stimuli.

The estimate of 35–70 μV for the signal range of the dark-adapted, red-sensitive cones at threshold is several times the

5–10 μV estimate for red-sensitive cones mediating an increment threshold detection. Measurements of intrinsic membrane noise of red-sensitive cones of *Pseudemys* are up to four times larger in darkness than in light, depending on the extent of interreceptor coupling¹². Thus the respective amplitudes of signals and noise underlying detection in darkness and in light have the appropriate relationship to suggest that the observed visual thresholds could be the result of a form of signal-to-noise discrimination of neural events that originate in the photoreceptors.

Our results indicate that each red-sensitive cone under the 2.35° stimulus spot effectively uses at least one photon, and possibly two. Under the conditions for which thresholds were obtained it would seem to matter very little whether or not the photoreceptors were electrically coupled in terms of their signals, for they would develop about the same photovoltage in either case, since a large number of adjacent cones are on the average absorbing the same number of photons. However, since coupling reduces noise in a given cone¹², the net effect of coupling would be to improve the signal-to-noise ratio during the detection of light under any condition for which a large number of coupled cones are stimulated.

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Endocrine differentiation of the fetal rabbit ovary in culture

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Although virilisation of the male fetus is accomplished in large part by the secretion of testosterone from the testis during embryogenesis¹, little is known about the function, if any, of the fetal ovary in female embryonic development. On the basis of studies in rabbits, in which castrate fetuses developed as phenotypic females, Jost concluded that the ovary does not have an active role in sexual differentiation². However, we have demonstrated that the onset of oestrogen formation in the fetal ovaries of rabbit and man occurs at approximately the same time that the fetal testis develops the capacity to form androgens^{3,4}, and Mauleon *et al.*⁵ have demonstrated that the fetal sheep ovary secretes 17 β -oestradiol before the onset of testosterone synthesis by the testis. These findings suggest that ovarian function is important during embryonic development. In the fetal rabbit, the onset of testosterone synthesis in the testis coincides with the appearance of 3 β -hydroxysteroid- $\Delta^4,5$ -isomerase activity^{3,6,7}. The mechanism regulating the time of appearance and the amount of this activity remains unclear, although the enzyme develops in fetal gonads cultured in chemically defined medium⁷, suggesting that the regulation of testosterone synthesis is intrinsic to the fetal testis. To gain insight into the factors responsible for the onset of endocrine function of the ovary we have compared the enzymatic development of embryonic rabbit ovaries and testes in organ culture. The results indicate that the enzymatic differentiation of fetal ovaries is also independent of hormonal induction and occurs in culture at the same time as endocrine differentiation of the fetal ovary *in vivo*.

On day 16 of gestation (the day of observed copulation was designated day 0), New Zealand white rabbits were killed, the embryos were removed aseptically, and the gonads with adjacent mesonephros were dissected from the embryos. Pairs of gonads from individual embryos were cultured at 37 °C in Serumless Medium (Gibco) in a humidified atmosphere of 5% CO₂ in air in separate wells (1.6 cm diameter) of a Linbro plate (Flow Laboratories). Media were changed at 48 h, and fetal gonads and media were collected at the times indicated in the figure legends. The genetic sex of each embryo was determined by staining the amniotic membrane with thionin to show the presence or absence of sex chromatin by the method of Klinger and Ludwig⁸. All gonads in which corresponding amniotic membranes were sex chromatin positive were designated ovaries.

To assess the enzymatic differentiation of fetal testes and ovaries we measured the conversion of 1,2-³H-dehydroepiandrosterone (54.7 Ci mmol⁻¹) to androstenedione, testosterone and 17 β -oestradiol in a total volume of 0.2 ml Serumless Medium. Depending on the developmental stage, two to eight fetal ovaries or one to eight fetal testes (representing 0.05–0.1 mg protein) were used in each incubation. After incubation,

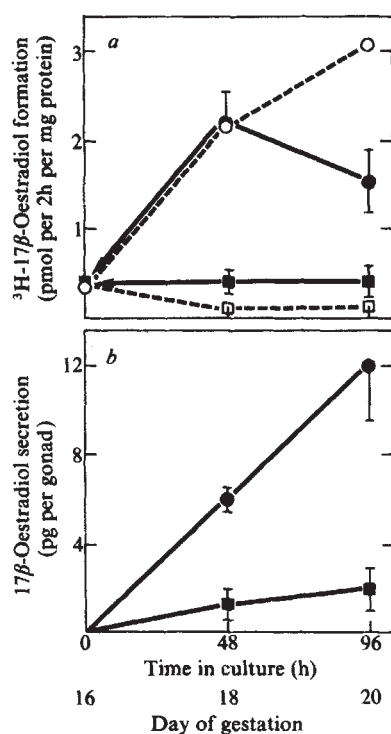


Fig. 1 Developmental pattern of 17 β -oestradiol formation and secretion by cultured and *in vivo* control gonads. *a*, ³H-17 β -oestradiol synthesis. Cultured fetal gonads were collected 48 and 96 h after the initiation of cultures, dissected free of mesonephric tissue, and incubated with 5 μ M 1,2-³H-dehydroepiandrosterone as described in the text. The ³H-17 β -oestradiol formed during incubation was purified as before⁴. Rates for *in vivo* control gonads are expressed as the mean of two observations, and the values for cultured gonads are expressed as the mean $\pm$ s.e.m. for four observations. ○, *In vivo* control ovaries; □, *in vivo* control testes; ●, ovaries; and ■, testes cultured from day 16 of gestation. *b*, 17 β -oestradiol secretion into the culture medium. Media from either ovarian or testicular cultures were pooled separately when the media were changed (48 or 96 h). Each pooled sample was extracted with 5 volumes of ethyl ether and chromatographed on Celite columns as before³. Aliquots corresponding to 25% of the column eluates for 17 β -oestradiol were assayed by radioimmunoassay¹⁰. Each sample represents the pooled media from 6–15 pairs of gonads, and the results are expressed as the mean and range of two experiments. ●, Ovaries; ■, testes.

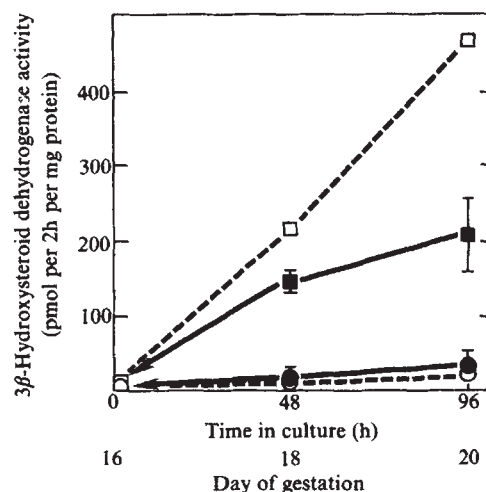


Fig. 2 3 β -Hydroxysteroid dehydrogenase activity in cultured and control fetal rabbit gonads. 3 β -Hydroxysteroid dehydrogenase activity was estimated by assessing the amount of androstenedione plus testosterone formed in the incubations of fetal gonads with 1,2-³H-dehydroepiandrosterone described in the text and the legend to Fig. 1. ○, *In vivo* control ovaries; □, testes; ●, ovaries; and ■, testes cultured from day 16 of gestation. Data for *in vivo* control gonads represent the mean of two experiments, and data for the cultured gonads represent the mean $\pm$ s.e.m. of four observations each.

appropriate ¹⁴C-labelled steroids were added in trace amounts to assess recovery, and the samples were extracted and chromatographed as before⁴. Protein was determined by a modification⁷ of the method of Lowry *et al.*⁹. Each of the steroids isolated by column chromatography was purified through several thin-layer chromatographic steps, and the authenticity of the isolated products was confirmed by recrystallisation. In addition we measured by radioimmunoassay¹⁰ the 17 β -oestradiol secreted into the media from ovarian and testicular cultures.

At day 16 of gestation neither fetal ovaries nor fetal testes synthesised 17 β -oestradiol from ³H-dehydroepiandrosterone (Fig. 1a). However, after 48 h in culture, fetal ovaries developed the capacity to form 17 β -oestradiol at a rate equal to that in control ovaries of corresponding age (2.2 pmol per 2 h per mg protein in cultured ovaries; 2.1 pmol per 2 h per mg protein in day 18 *in vivo* control ovaries). The rate of 17 β -oestradiol formation in cultured ovaries declined by 96 h to 1.15 pmol per 2 h per mg protein but remained substantially greater than the rate of formation in both cultured and day 20 *in vivo* control testes. Furthermore, after 48 and 96 h in culture, ovaries secreted four to six times more 17 β -oestradiol per gonad into the medium than did testes (Fig. 1b), indicating that the observed enzymatic differentiation *in vitro* reflects a true functional oestrogen synthesis similar to that which occurs *in vivo*¹⁰.

3 β -Hydroxysteroid dehydrogenase activity was estimated by measuring androstenedione and testosterone formation from 1,2-³H-dehydroepiandrosterone in the same fetal tissues used for the assessment of 17 β -oestradiol formation. At the time of explantation (day 16 of gestation) 3 β -hydroxysteroid dehydrogenase activity was low in both ovaries and testes (<3 pmol per 2 h per mg protein). There was a progressive increase in 3 β -hydroxysteroid dehydrogenase activity in both ovaries and testes throughout the 4-day culture period (Fig. 2), although the final rate was greater in testes than ovaries (209 and 37 pmol per 2 h per mg protein, respectively).

Although the histological and enzymatic differentiation in culture of the fetal testis of rat¹¹ and rabbit⁷ have been described before, our study shows for the first time the enzymatic differentiation of the fetal ovary in culture. ³H-dehydroepian-

drosterone was used as substrate to enable us to measure simultaneously the development of the rate-controlling enzyme for testosterone synthesis (namely 3β -hydroxysteroid dehydrogenase- Δ^4 -isomerase) and the capacity for 17β -oestradiol synthesis in the fetal rabbit gonad⁶. Although this procedure may underestimate the enzymatic capacity for oestrogen synthesis, the fact that the secretion of 17β -oestradiol into the medium by cultured ovaries parallels the increase in oestrogen formation from ^3H -dehydroepiandrosterone indicates that the differences in oestrogen formation between the fetal ovary and testis are real. Furthermore, similar measurements were obtained after short term incubation of fetal gonads when a saturating concentration of ^3H -testosterone was used as substrate for oestrogen synthesis³.

The fact that endocrine differentiation of the fetal rabbit ovary, as well as the testis, occurs in organ culture at the same time that the process occurs *in vivo* suggests that the differentiation is inherent to the gonads and not controlled by extragonadal factors. Because enzymatic differentiation of the fetal ovary occurs earlier than would be predicted on the basis of histological criteria in rabbit³, man⁴ and sheep⁵ it is possible that the onset of 17β -oestradiol synthesis is a prerequisite for other events in ovarian differentiation. If that is true, the genetic

composition of the female may be responsible for the development of endocrine function in the female embryo, and the endocrine function in turn may be responsible for the histological differentiation of the ovary. Regardless of any endocrine implications, the demonstration that enzymatic markers for fetal ovaries and testes develop *in vitro* will be useful in the study of factors controlling gonadal differentiation.

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Lactogenic receptor regulation in hormone-stimulated steroidogenic cells

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Receptor sites for lactogenic hormones such as prolactin (PRL), human growth hormone (HGH), and placental lactogens, are widely distributed in mammalian tissues, including mammary glands¹, steroid-secreting cells of the adrenal, testis, and ovary, and target cells of steroid hormone action such as liver, prostate, and kidney^{2,3}. Although the biological functions of lactogen binding sites remain uncertain, a relationship between prolactin and lipoprotein metabolism is implied by the occurrence of prolactin receptors in steroidogenic cells of the gonads and adrenal, and by the ability of prolactin to increase esterified cholesterol in the testis⁴. Recently, loss of testicular prolactin receptors has been observed following elevation of circulating luteinising hormone (LH) concentrations by the gonadotropin releasing hormone (GnRH) and its agonist analogues^{5,6}. The hormone dependence of lactogen receptor sites in steroid-secreting cells was further analysed in rat testis, ovary, and adrenal glands after treatment with the respective trophic hormones, gonadotropin and ACTH. In each of these tissues, rapid and transient loss of lactogen receptors was observed after trophic hormone stimulation. These findings indicate that increased turnover of lactogen receptors is an important component of the target-cell response, and suggest that prolactin receptors might be involved in the transport of lipoprotein precursors for steroid biosynthesis.

Previous studies have shown that treatment with exogenous gonadotropins such as ovine LH (oLH) or human chorionic gonadotropin (HCG) causes marked and prolonged reduction of testicular LH receptors^{7–9}. This process of receptor depletion, commonly referred to as down-regulation, is analogous to the

effects of other peptide hormones, such as insulin and growth hormone, on their specific receptor sites^{10,11}. We have recently observed that lactogen receptors in the testis initially undergo changes in parallel with those of LH receptors after gonadotropin treatment. An early brief rise in both receptor sites is followed by a marked and transient decrease of lactogen receptors after administration of oLH or HCG¹². An example of the concomitant loss of testicular LH and lactogen receptors after treatment with gonadotropins is shown in Fig. 1. The lactogen receptors were decreased by 70% at 24 h, and returned to normal values at 48 h, whereas LH receptors fell rapidly and remained low for up to 96 h. The reduction in lactogen binding followed the peak of testosterone secretion, which normally occurs within 4 h after administration of either GnRH or exogenous gonadotropin. The disappearance of lactogen receptors was not due to occupancy of the binding sites by endogenous hormone, since no significant increase in serum prolactin was detected by radioimmunoassay after LH treatment. In addition, no change in degradation of labelled HGH was observed in testis fractions prepared from gonadotropin-treated rats.

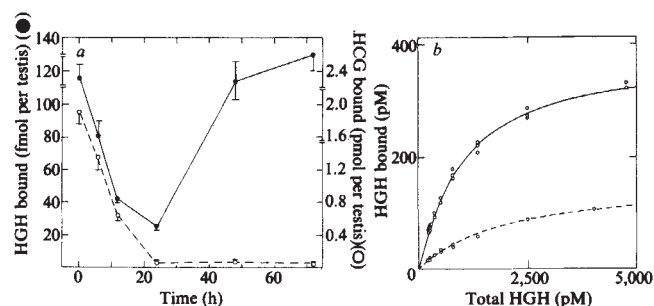


Fig. 1 *a*, Transient loss of lactogenic hormone binding sites in adult rat testes stimulated *in vivo* by administration of 20 µg HCG. A 15,000g fraction of testis homogenate was analysed for receptor binding capacity with ¹²⁵I-HGH and ¹²⁵I-HCG to quantitate lactogenic and LH receptors, respectively^{6,20}. The use of HGH tracer to measure lactogen receptors was based on the ability of HGH to bind specifically to receptors for prolactin and other lactogens¹. In this and subsequent figures, each point represents the mean $\pm$ s.e. of data from groups of six rats. The mean $\pm$ s.e. for the control animals throughout the study are shown in double horizontal bars on the vertical axes. *b*, Saturation curves for ¹²⁵I-HGH binding to 15,000g fractions of homogenates from control testes (continuous line) and testes removed 24 h after administration of 100 µg oLH (broken line).

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Table 1 Insulin receptors in the rat ovary during stimulation with HCG

Time after injection with HCG	Insulin receptors (fmol per mg protein; mean $\pm$ s.e.)
0 (control)	38.8 $\pm$ 0.35
6 h	37.4 $\pm$ 1.5
12 h	37.9 $\pm$ 7.9
24 h	35.6 $\pm$ 0.3
48 h	27.4 $\pm$ 4.5

Primed rats were injected subcutaneously with 20 μ g of HCG and groups of three rats were sacrificed at the times indicated. Pairs of ovaries were assayed for insulin receptor sites using 125 I-insulin. Two aliquots in duplicate of the 15,000g pellet of ovarian membranes were incubated for 16 h at 4 $^{\circ}$ C with 1.27×10^{-10} M insulin, specific activity 1,325 c.p.m. per fmol. Similar aliquots were incubated in the presence of 5×10^{-7} M unlabelled insulin to determine nonspecific binding.

In the luteinised rat ovary, similar changes in lactogen receptors were observed after gonadotropin treatment. When immature rats, primed with pregnant mare serum gonadotropin (PMSG) and HCG to induce luteinisation of the ovaries¹³, were treated with 20 μ g HCG, the rapid and marked fall in LH receptor capacity was consistently accompanied by a decrease in binding of 125 I-HGH. This decrease in lactogen sites occurred earlier than in the testis and was again coincident with LH receptor loss between 6 and 24 h. The lactogen receptors had returned to normal at 48 h, whereas marked loss of LH receptors persisted for 3 d (Fig. 2). During these gonadotropin-induced changes in lactogen receptors, there was no alteration in the concentrations of two other luteal cell receptors, for insulin and β -adrenergic ligands. As shown in Table 1, insulin receptors in the luteinised ovary remained constant after HCG treatment that caused marked decreases in LH and lactogen receptors. There was a similar lack of effect of HCG treatment on β -adrenergic receptors, which have recently been shown to be functionally coupled to adenylate cyclase and progesterone secretion in the luteal cell¹⁴.

Gonadal lactogenic hormone receptors, like those for LH, are located on the steroidogenic cells of the testis¹⁵ and ovary¹⁶. The common location of testicular LH and prolactin sites, and the similarity in their rates of depletion after GnRH or LH/HCG treatment, suggest that down-regulation of the two receptors is coordinated after gonadotropin stimulation, and that the two receptors could be physically related within the target cell membrane. Although the LH and prolactin sites are highly specific for the respective ligands, the molecular weights of the two receptors are similar after detergent solubilisation (about 200,000)^{17,18}. This was further examined by simultaneous gel filtration of the two binding sites on 6% agarose after extraction from testis interstitial particles with 1% Triton X-100. Subsequent binding assay of the free receptors in each fraction with 131 I-HCG and 125 I-HGH revealed two coincident peaks of hormone-binding activity with K_{av} of 0.31, consistent with a molecular radius of about 6.8 nm for each of the detergent-solubilised hormone receptors.

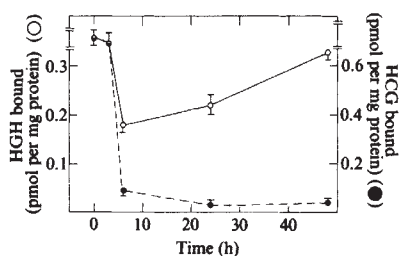


Fig. 2 Binding of lactogen (HGH) (○) and gonadotropin (HCG) (●) to the 15,000g fraction of homogenates from luteinised rat ovaries after subcutaneous treatment with 20 μ g HCG given 8 d after priming with PMSG and HCG. Binding assays were performed as previously described^{6,13}

In the adrenal cortex, prolactin receptors have been localised to the reticularis and fasciculata zones¹⁹. Following treatment of male rats with corticotropin (ACTH₁₋₂₄), we observed a marked reduction in adrenal lactogen binding between 6 and 12 h after injection of the hormone (Fig. 3). Although the return of adrenal receptors was more rapid than in the testis and ovary, the initial phase of receptor loss was again subsequent to the peak of steroid (corticosterone) secretion, which usually occurs within 60–90 min of ACTH administration.

The decreased binding of HGH tracer by steroid-secreting cells of the gonads and adrenal after hormonal stimulation was shown by analysis of the data²⁰ to result from loss of lactogen receptors, rather than a change in the association constant (Table 2). In addition, hormone-induced depletion of lactogenic sites appeared to be cell-specific, since gonadotropin stimulation had no effect on adrenal or prostatic lactogen binding, and ACTH did not alter the testicular lactogenic sites. As noted above, prolactin receptor loss was not attributable to elevated serum prolactin levels. Recently, a rapid and transient phase of prolactin receptor loss has been described in the mammary gland and liver²¹ after treatment with large doses of prolactin, preceding the rise in receptor concentration that results from long-term prolactin treatment²². However, the reduction of lactogenic hormone sites we observed after heterologous hormone treatment presumably involves loss of unoccupied binding sites, in contrast to the usual form of receptor down-regulation in which occupancy initiates receptor loss by processing or degradation.

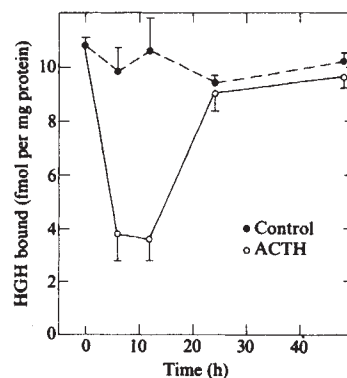


Fig. 3 Rapid loss and recovery of lactogen binding sites in rat adrenal glands after treatment with 10 units of ACTH₁₋₂₄ (○) compared with binding to control adrenals from untreated rats (●). After decapsulation, adrenal glands were homogenised prior to binding analysis with 125 I-HGH.

Several explanations can be suggested for these observations on the rapid regulation of lactogenic receptors in steroid-secreting cells. In the gonads, the similar molecular size and coordinate regulation of the LH and lactogen receptors is compatible with a close physical relationship between the two sites. However, while occlusion of the lactogenic sites could be envisaged during occupancy of the gonadotropin receptors, no such cross-reaction has been observed during specificity studies on LH and prolactin receptors. Also, the more rapid return of the lactogenic sites demonstrates their ability to vary independently of LH receptors. It is also conceivable that the loss of prolactin receptors after hormonal stimulation of the gonads and adrenal is part of a more generalised effect on plasma membrane receptor turnover. However, this possibility is rendered unlikely by the absence of changes in luteal cell receptors for insulin and catecholamines during HCG-induced loss of lactogen receptors.

The receptor loss observed after *in vivo* stimulation of steroidogenesis may be related to an effect of high steroid concentration at the cell membrane, since reduction of adrenal

Table 2 Characterisation of lactogenic binding sites in steroid secreting cells in the basal and stimulated state

Receptor location (treatment)	Equilibrium association constant ($K_a \times 10^9 \text{ M}^{-1}$)*		Binding capacity for HGH (fmol per mg protein)*	
	Controls	Stimulated	Controls	Stimulated
Testis (24 h after oLH—100 µg)	1.3 ± 0.06	0.9 ± 0.06	22.5 ± 0.5	8.8 ± 0.4
Adrenal (6 h after ACTH—1 IU)	1.0 ± 0.15	0.8 ± 0.2	555 ± 45	154 ± 18
Ovary (6 h after HCG—20 µg)	1.2 ± 0.05	1.2 ± 0.06	540 ± 30	243 ± 10

* All values are mean ± s.e.m.

and kidney prolactin receptors follows high dosage treatment with dexamethasone and sex steroids²³. However, the loss of prolactin receptors in hormone-stimulated gonads and adrenals occurs after the phase of steroid secretion, and is not prevented by treatment with inhibitors of steroidogenesis (unpublished observations). A transient steroid-induced blockade of protein synthesis could also contribute to lactogen receptor loss, since hepatic prolactin receptors undergo transitory loss after cycloheximide treatment²⁴, and the early actions of ACTH have been shown to include decreased protein synthesis in the adrenal gland²⁵.

The most likely explanation of lactogen receptor loss is that stimulation of internalisation is a consequence of trophic hormone action on the steroidogenic target cell²⁶. Such internalisation of prolactin receptors may be an important consequence of the activation process, particularly if related to the uptake of precursors for steroidogenesis. This mechanism need not be responsible for provision of the cholesterol immediately metabolised during hormone-induced steroid secretion, but would be important for the long-term maintenance of precursor pools within the target cells of the gonads and adrenal. The major substrate for biosynthesis of steroid hormones in the testis, ovary and adrenal glands of the rat is circulating lipoprotein cholesterol, rather than cholesterol that is newly synthesised within the steroid secreting cell²⁷. In rats, high density lipoproteins bind to the steroidogenic cell membrane²⁸ and may be internalised as described for the low density moiety in human cells²⁹.

A prolactin receptor-mediated mechanism controlling lipoprotein transport would be consistent with the relationship between prolactin and cholesterol metabolism in the gonads⁴, and with the high content of prolactin receptors in the ovary, testis, and adrenal gland. Recently, the prolactin molecule has been demonstrated within ovarian luteal cells and adrenal fasciculata cells³⁰, presumably after receptor binding and internalisation. Furthermore, in the hepatocyte, where lipoprotein synthesis occurs³¹, prolactin receptors undergo rapid turnover²⁴ and a high proportion of the sites are intracellular³². In the lactating mammary gland, where lipoproteins are actively metabolised, prolactin receptors are abundant¹ and have been detected within epithelial cells³³. This evidence for the presence of prolactin receptors within sterol metabolising cells, with the present finding of increased receptor turnover after hormone stimulation, is consistent with the proposal that prolactin receptors could be involved in a mechanism for regulating the entry of lipoprotein precursors in to steroid secreting cells.

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HLA-restricted T-cell recognition of Epstein-Barr virus-infected B cells

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In mice the cytotoxic T-cell response to several types of virus is influenced by genes within the major histocompatibility complex^{1–5}; in particular, genetic control is exercised at the effector cell level through a requirement that virus-specific cytotoxic T cells recognise viral antigens in association with H-2K and H-2D region gene products on the surface of infected cells^{1,2}. In man the restriction which the analogous HLA-A, -B and -C-region gene products might place on virus-specific T-cell function is still in dispute. The earliest and most controversial evidence concerns the Epstein-Barr virus (EBV), a B lymphotropic agent which causes infectious mononucleosis⁶ (IM) and which induces an unusually vigorous T-cell response⁷; cytotoxic T cells from IM patients' blood were shown to be EBV-specific, yet, in contrast to mouse systems, apparently free of any obvious HLA restriction^{8,9}. Since then T-cell recognition of EBV-infected B cells has assumed particular significance as a model system for the study of cytotoxic T-cell function in man. This report describes the results of a new approach clearly indicating that HLA-A and -B region products do indeed have a role in this system.

During recent experiments monitoring the ease of establishment of EBV-transformed B-cell lines from cultures of adult donor leukocytes exposed to the virus *in vitro*, it was found that cultures from non-infected (seronegative) individuals regularly gave rise to cell lines, whereas in the corresponding cultures from previously-infected (seropositive) donors the early proliferation of virus-infected B cells was halted by a T-cell dependent mechanism¹⁰. All the available evidence suggested that this regression of growth was occurring through the reactivation *in vitro* of a pool of EBV-specific cytotoxic T-cell precursors present exclusively in the blood of seropositive individuals^{11,12}. In

the experiments reported here T cells collected from regressing cultures have been tested for their ability to inhibit the outgrowth of EBV-transformed B cells of the autologous line and of HLA-related and unrelated allogeneic lines.

Ten healthy adult donors of known HLA type and of known serological status with respect to EBV were used. Experimental procedures were as previously described¹⁰⁻¹². From each 60-ml blood sample, 7×10^6 mononuclear cells were used in a microtest plate assay for which the cells were exposed to EBV, or to culture medium as a control, before seeding in 0.15-ml volumes into microtest plate wells at one of a range of concentrations (2×10^6 to 1.25×10^5 cells per ml); the cultures were then observed for 28 d to assess the 'strength' of regression for each donor in terms of the minimum initial concentration required for a 50% incidence of the effect among replicate cultures¹⁰. The remaining mononuclear cells were exposed to EBV, cultured at 2×10^6 per 2-ml well and then 10–14 days later the cultures were collected and the T-cell subpopulation prepared. Aliquots of 10^5 T cells were then added to microtest plate wells containing known numbers (ranging from 2×10^5 to 2.5×10^2) of autologous or of allogeneic EBV-transformed target cells of known HLA type; three to five replicate wells were set up for each particular combination, along with parallel cultures of target cells alone. After 2 weeks the incidence of successful outgrowth of the target cells could be scored unequivocally¹² and, for each particular effector and target cell combination, the growth inhibitory effect of the T cells was expressed as the ratio of that number of target cells required for a 50% incidence of successful outgrowth in the presence of T cells, to that number required in cultures of target cells alone.

Table 1 summarises the data from all 10 donors studied. The results clearly emphasise the immunological basis of regression in that the effect was consistently observed in cultures set up from all seven seropositive donors tested, with individual donors tending to show either strong (CA, SG, BW) or somewhat weaker (MM, AR) responses on repeated testing, but was never seen in cultures from the seronegative donors. This pattern of results was exactly reflected in the co-cultivation assay where T cells collected from seropositive donor cultures just before their regression consistently showed a marked inhibition of outgrowth of the autologous EBV-transformed cell line, whereas very little growth inhibition was apparent in the corresponding co-cultures from three seronegative donors.

Allogeneic cell lines used as targets in the co-cultivation assay were likewise hardly affected by the addition of T cells from seronegative donor cultures; in contrast effector cells from seropositive donor cultures did in some cases cause significant inhibition, although this was almost invariably less than that mediated by these same cells against their autologous cell line. Using the degree of autologous target cell inhibition within each experiment as a standard, the relative inhibition suffered by allogeneic cell lines was analysed in the light of their known HLA-A, -B and -C antigen expression. This approach revealed an underlying pattern in the results which is illustrated by the representative data shown in Fig. 1 from three seropositive donors, CA, MM and SG. Whilst an analysis in relation to HLA-C antigen expression is difficult in view of the incomplete typing at this locus, there are strong indications that sharing of HLA-A or -B antigens between effector and target cells predisposes towards significant cross-reactivity. Thus inhibition of

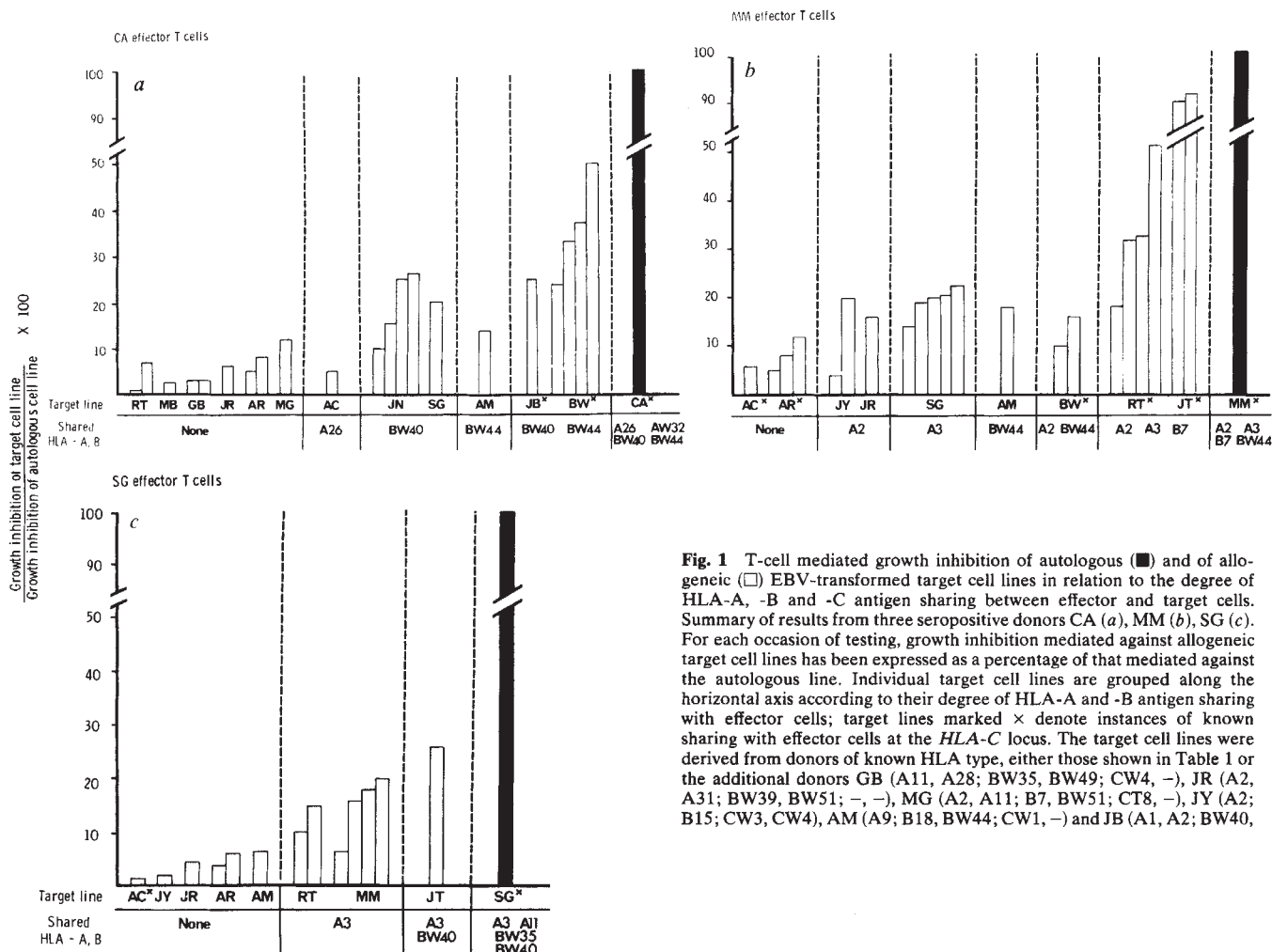


Fig. 1 T-cell mediated growth inhibition of autologous (■) and of allogeneic (□) EBV-transformed target cell lines in relation to the degree of HLA-A, -B and -C antigen sharing between effector and target cells. Summary of results from three seropositive donors CA (a), MM (b), SG (c). For each occasion of testing, growth inhibition mediated against allogeneic target cell lines has been expressed as a percentage of that mediated against the autologous line. Individual target cell lines are grouped along the horizontal axis according to their degree of HLA-A and -B antigen sharing with effector cells; target lines marked × denote instances of known sharing with effector cells at the HLA-C locus. The target cell lines were derived from donors of known HLA type, either those shown in Table 1 or the additional donors GB (A11, A28; BW35, BW49; CW4, -), JR (A2, A31; BW39, BW51; -, -), MG (A2, A11; B7, BW51; CT8, -), JY (A2; B15; CW3, CW4), AM (A9; B18, BW44; CW1, -) and JB (A1, A2; BW40,

Table 1 EBV-specific effector T-cell assays for donors of known HLA type and antibody status with respect to EBV

Donor* (Antibody status to EBV)				Effector T-cell assays		
	HLA type†			No. of experiments	Cell concentrations for 50% regression‡	Growth inhibitions of autologous cell line§
CA (+)	A26 AW32;	BW40 BW44;	CW3 CW5	4	4.8×10^5 cells ml ⁻¹	170
MM (+)	A2 A3;	B7 BW44;	CW5 CT8	6	7.3×10^5 cells ml ⁻¹	38
SG (+)	A3 A11;	BW35 BW40;	CW2 CW4	4	3.3×10^5 cells ml ⁻¹	120
BW (+)	A2;	BW40 BW44;	CW3 CW5	5	3.2×10^5 cells ml ⁻¹	108
JN (+)	AW24 AW33;	B8 BW40;	—	4	8.3×10^5 cells ml ⁻¹	79
AR (+)	A1;	B8 B17.1;	CW6 CT8	6	7.5×10^5 cells ml ⁻¹	15
JT (+)	A2 A3;	B7 BW40;	CW6 CT8	1	8.0×10^5 cells ml ⁻¹	20
RT (-)	A2 A3;	B7 B15;	CT8 —	3	$>2.0 \times 10^6$ cells ml ⁻¹	2
AC (-)	A1 AW26;	B8 BW45;	CW6 CT8	2	$>2.0 \times 10^6$ cells ml ⁻¹	2
MB (-)	A1 A3;	B8 B14.2	—	1	$>2.0 \times 10^6$ cells ml ⁻¹	3

* Antibody status with respect to EBV was determined by the anti-virus capsid antigen immunofluorescence test as described elsewhere¹⁰.

† Typing at the HLA-A, -B and -C loci was carried out on freshly isolated blood mononuclear cells at the National Tissue Typing Reference Laboratory. Undefined C locus antigens are shown as blanks.

‡ The minimum initial cell concentration for a 50% incidence of regression was calculated from the incidence of transformation and/or regression seen in replicate cultures in the 4-week microtest plate assay¹⁰. Mononuclear cells were exposed either to culture medium alone or to an EBV preparation (10^5 50% transforming doses per ml) from B95-8 culture supernatant before seeding in 0.15-ml volumes into microtest plate wells (Nunc) at 2×10^6 , 10^6 , 5×10^5 , 2.5×10^5 and 1.25×10^5 cells per ml and culturing for 4 weeks. The figure given for each donor is the mean of those obtained in the number of experiments shown. A value of $>2 \times 10^6$ cells per ml indicates that regression was not seen in any of the cultures.

§ EBV-infected mononuclear cell cultures in 2-ml wells (Linbro) were collected 10–14 d post infection and dead cells removed by a preliminary centrifugation for 30 min at 400g on Ficoll-Hypaque. The T-cell subpopulation was then prepared by rosetting with AET-treated sheep erythrocytes according to the method of Gmelig-Meyling and Ballieux²² and the rosetted cells rescued by lysis of the erythrocytes in 0.75% NH_4Cl in 0.016M Tris buffer, pH 7.25, at 4 °C. Aliquots of 10^5 such T cells were added to replicate microtest plate wells containing known numbers (2×10^5 , 10^5 , 5×10^4 , 2.5×10^4 , 10^4 , 5×10^3 , 2.5×10^3 , 10^3 , 5×10^2 and 2.5×10^2) of target cells of the autologous EBV-transformed B-cell line and the incidence of successful target cell outgrowth was recorded after 2 weeks¹². T-cell mediated growth inhibition was expressed as the ratio of that number of target cells required for a 50% incidence of successful outgrowth in the presence of T cells to that number required for successful outgrowth in cultures of target cells alone. The figure given for each donor is the mean of those obtained in the number of experiments shown.

growth over and above that seen against HLA-unrelated targets was consistently found in some, though not all, examples of a single shared antigen (for example, reciprocal recognition of MM and SG through shared A3, Fig. 1b, c), whereas more extensive antigen sharing was almost always associated with an enhanced cross-reactivity. For instance, the recognition of BW targets by CA effectors through shared BW40, BW44 (Fig. 1a) and of JT targets both by SG effectors through shared A3, BW40 (Fig. 1c) and by MM effectors through A2, A3, B7 (Fig. 1b) was in each case confirmed by the reciprocal target and effector cell combination (data not shown).

It seems most unlikely that results of this type could have arisen by chance or could be explained on the basis of differences in the essential sensitivity to growth inhibition *per se*. Thus, whilst individual results from such a small sample of randomly selected donors must be interpreted cautiously, the overall data are consistent with the concept of an HLA-related T-cell cytotoxicity similar to that recently reported for influenza virus-specific human T cells, again studied after secondary stimulation *in vitro*¹³. Furthermore, the apparent relationship between the magnitude of effector cell function and the extent of HLA antigen sharing with target cells suggests that the effector cell population contains a number of independent clones, each recognising the target antigen in association with one particular HLA region gene product. Within this framework there are individual examples of poor recognition despite HLA antigen sharing (for example, CA effectors and AC targets sharing A26, Fig. 1a) and such exceptions, perhaps related to those now being recognised in the influenza virus system^{14–16}, require further investigation.

The rapid inhibition of growth caused by effector T cells in the co-cultivation assay¹² is almost certainly a consequence of their direct cytotoxic action. Thus chromium release assays carried out in this¹⁷ and in another¹⁸ laboratory have now shown that effector T cells from regressing cultures are both cytotoxic and EBV-specific, as they kill autologous EBV-transformed cells but not autologous pokeweed mitogen-stimulated B lymphoblasts or cells of the K562 cell line, a sensitive indicator of nonspecific natural killer cell activity¹⁹. If, as seems likely, these reactivated T cells recognise the same EBV-associated cell surface change as do primary effector T cells present in the blood

of acute IM patients (that is, the lymphocyte-detected membrane antigen, LYDMA⁸) it becomes important to re-examine the possibility of HLA-related constraints governing IM T-cell cytotoxicity^{20,21}. Certainly this work and other independent studies¹⁸ strongly suggest that cytotoxic T cells reactivated *in vitro* do indeed recognise an EBV-associated LYDMA-like antigen in conjunction with HLA-A and -B region gene products on the surface of infected B cells. This conclusion is strengthened by our most recent experiments demonstrating that such recognition can be specifically blocked by pretreatment of the target cells with high titre preparations of monoclonal antibodies to a common determinant on HLA-Ag, -B and -C molecules.

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Hyperpolarisation of rat peritoneal macrophages phagocytosing latex particles

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The changes that take place in the plasma membrane during endocytosis are still poorly understood¹. Studies of the electrical properties and related permeabilities of cells during pinocytosis and phagocytosis should provide insight into these changes. This approach has not been much exploited, although there have been a few relevant reports. For example, induction of pinocytosis in amoebae produces a marked decrease in plasma membrane resistance², and exposure of polymorphonuclear leukocytes to phagocytosable particles can engender alterations in ionic permeabilities³. The present report demonstrates that the induction of phagocytosis in rat peritoneal macrophages is accompanied by a sustained hyperpolarisation of the cells.

Macrophages were obtained by the implantation of agar-coated sterile Teflon disks in the peritoneal cavities of Wistar rats⁴. After 3 d the disks were removed and placed in Tyrode solution (NaCl, 124 mM; KCl, 3 mM; CaCl₂, 2.5 mM; MgCl₂, 1.2 mM; NaHCO₃, 15 mM; NaH₂PO₄, 1.2 mM; glucose, 5 mM, pH 7.4, kept at 37 °C with 95% O₂–5% CO₂ bubbling through). The disks were placed in an electrophysiological chamber and macrophages were selected with an inverted phase microscope. The cells were penetrated with glass microelectrodes of less than 0.5 µm diameter filled with 3 mM KCl. Electrode resistances were in the range of 20–50 MΩ and tip potentials were less than 5 mV. The microelectrodes were coupled through a high impedance compensator to a differential preamplifier MZ4 (Nihon-Khodon) and a VC-8 oscilloscope (Nihon-Khodon). Records were photographed with a cine camera running at velocities of 10 or 20 mm s⁻¹.

As in previous work by our laboratory^{5–7}, most of the cells penetrated showed distinct, negative potentials (Fig. 1a) which disappeared when the electrodes were withdrawn. For the 200 cells studied in the present work, the mean potential was -13 ± 4.7 (s.d.) mV. The potentials were stable for more than 30 min, but disappeared on addition of 2 mM NaF or 2.5 mM DNP. They were similar to the potentials we have obtained previously, and to those reported for macrophages of other species^{8,9} and for other non-excitable cells^{10–14}. Occasionally cells in our preparations showed positive potentials whose nature is under study and will not be discussed here.

Difco latex (0.8 µm diameter spheres, washed and diluted 1:10 in phosphate-buffered saline: NaCl, 137 mM, KCl, 2.7 mM, buffered at pH 7.2–7.4 with 10 mM sodium phosphate) was added to the disks in the chamber (0.06 ml of latex added to 20 ml of Tyrode). Latex induces extensive phagocytosis which persists for at least 20–30 min¹⁵. During this time, approximately 10 particles per cell are taken up. Latex was added to impaled cells 2–3 min after they had been penetrated. When this was done there was a rapid hyperpolarisation (Fig. 1b) followed by a gradual hyperpolarisation which reached a maximum at 15–30 min (Fig. 1c). The mean initial potential measured in the first minute after exposure to latex was -25 ± 3.2 and the eventual hyperpolarisation was -46 ± 5.1 mV (40 cells). After 20–30 min, the membrane depolarised towards the pre-stimulation level (Fig. 1d). In 80% of the cells responding to latex we have observed short trains (< 1 s) of small (up to 5 mV) brief depolarisations and hyperpolarisations or slower oscillations of up to 2 mV and 3 s duration, superimposed on the longer term hyperpolarisation. Addition of phosphate-buffered

saline without latex or of a drop of Tyrode solution does not provoke changes in the membrane potential.

Gallin and coworkers^{8,9} working on macrophages of other species have reported transient hyperpolarisations occurring spontaneously and in response to chemotactic factor isolated from serum. They have suggested that the hyperpolarisations might reflect increased permeability to potassium, perhaps through events in which calcium is involved. When we increased the concentration of calcium in our medium to 3.8 mM we observed an increase in the mean potential measured in unstimulated cells to -20 ± 2.2 mV (30 cells). With such cells latex evokes hyperpolarisation to -50 ± 4.3 mV (10 cells).

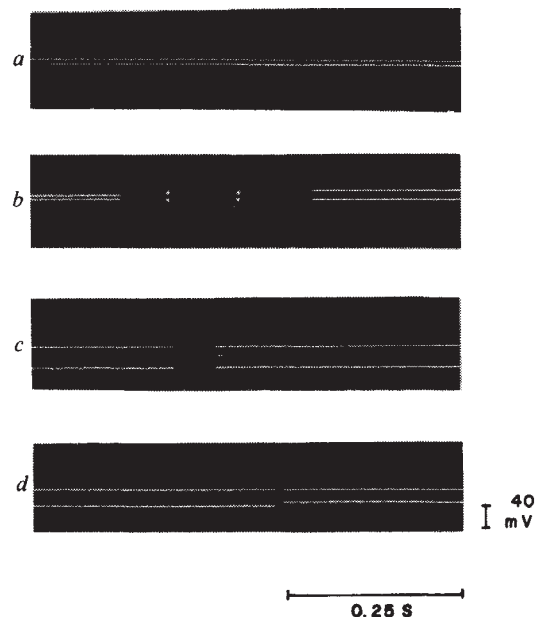


Fig. 1 Records obtained from the same cell at different stages in the response to latex. *a*, Entry of the electrode into the cell. *b*, Addition of latex. The traces on the left show the potential just before the addition of latex. The camera was then stopped, advanced two frames (producing the two pairs of dots to mark the time of addition of latex), latex was added and recording resumed 30 s later. The traces on the right thus show the potential 30 s after adding latex. A distinct hyperpolarisation has occurred. *c*, Potentials 15 (left) and 20 (right) min after adding latex. The camera was stopped between the two recording periods producing the gap in the record. Note the hyperpolarisation. *d*, Potentials 25 (left) and 30 (right) min after adding latex. The camera was stopped between the two recording periods producing the gap in the record. Note the decrease of the potential.

The present investigation and the studies cited above suggest that the early events in the induction of endocytosis include changes in the cell's permeability to ions. For granulocytes, it is reported that alterations in membrane potential can be induced by interaction of molecules that stimulate endocytosis with the cell surface; the potential changes do not require actual ingestion of the molecules¹⁶, but whether this is generally the case is not known. It is too early for us to speculate in detail on the significance of the changes we observe or on how the permeability changes are related to the various stages of endocytosis or to the properties of the cell-surface receptors involved (presumably in our case, relatively nonspecific receptors¹ are involved). However, given the many parts evidently played by ions such as Ca²⁺, K⁺ and so forth in controlling the distribution or functional state of such cellular elements as contractile proteins, there are many possibilities for their participation in influencing endocytic processes. In any event, the work reported

here suggests that electrophysiological techniques will prove useful in future analyses of cell-surface changes related to endocytosis by mammalian cells.

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Electrophysiological responses of *Didinium nasutum* to *Paramecium* capture and mechanical stimulation

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Didinium nasutum is a carnivorous ciliate with a preference for feeding on species of *Paramecium*. Accidental contact between a *Paramecium* and the proboscis of a hungry *Didinium* (Fig. 1a) causes instantaneous discharge of extrusive organelles from the proboscis. If the strike is successful, some of these organelles penetrate the *Paramecium*, which immediately stops swimming and discharges many trichocysts, mostly from the struck side (Fig. 1b). Cytoplasmic streaming pulls the discharged organelles inward, the captured *Paramecium* reaches the proboscis, and then the *Didinium* swallows the prey, opening its proboscis^{1–10} (Fig. 1c and d). On the other hand, a hungry *Didinium* does not discharge extrusive organelles when it collides with a glass wall. Instead it shows an avoiding reaction. When a *Paramecium* collides with the proboscis of a fed *Didinium*, the proboscis similarly does not discharge extrusive organelles, and the fed *Didinium* makes an avoiding response. We found that a hungry *Didinium* held steady by two glass capillary microneedles performed normal capture and ingestion in a solution containing *Paramecium caudatum*. We describe here an electrophysiological investigation of *Didinium nasutum* in collision with *P. caudatum* or with a glass rod while held still by glass capillary microneedles.

Methods of stimulation and recording were similar to those used by Naitoh and Eckert for electrophysiological investigations of *Paramecium*¹¹. Typical results are shown in Fig. 2. Accidental contact between a *Paramecium* and the proboscis of a fixed hungry *Didinium* generated a transient hyperpolarising potential of the *Didinium* cell, followed by a depolarising action potential associated with discharge of the extrusive organelles (Fig. 2a and b and Fig. 2c and d₂). The peak of the depolarising potential corresponded to completion of the discharge of the extrusive organelles. Subsequently, the membrane potential returned slowly to resting level. Marked fluctuations of the membrane potential often occurred during this period (Fig. 2c and d₂). Weak reversals of ciliary movement were associated with depolarisations of small magnitude. On rare occasions after discharging extrusive organelles, *Didinium* failed to capture the

target organism, possibly because of a poor hit. *Didinium* then simply withdrew the discharged extrusive organelles. Even in this case, the changes in membrane potential were similar to those occurring in cases of successful capture.

Mechanical stimulation of the apex of the proboscis of a hungry *Didinium* with a glass rod induced a transient depolarising mechanoreceptor potential, which was followed by a depolarising action potential of the general membrane (Fig. 2f and g). No discharge of extrusive organelles was observed, but the *Didinium* showed ciliary reversal in response to this stimulation. A spontaneous action potential was often recorded in *Didinium* cells (Fig. 2d₁), and this also caused ciliary reversal.

In some cases, the proboscis of a fixed fed *Didinium* happened to collide with a new *Paramecium* about 5 min after ingestion of the previous prey. In such cases, the membrane responses were the same as for mechanical stimulation of the proboscis of a fixed hungry *Didinium* (Fig. 2e). Fed *Didinium* never discharged extrusive organelles, but responded to contact with *Paramecium* by ciliary reversal, in the same way as to a glass rod.

The proboscis membrane of a hungry *Didinium* seems to have a chemoreceptor that responds to contact with *Paramecium*, as well as a mechanoreceptor able to sense external mechanical stimulation. Chemoreception induces a hyperpolarising potential, and mechanoreception induces a depolarising potential. On the other hand, only the mechanosensitive system of the proboscis membrane is active in a fed *Didinium*. According to Naitoh and Eckert, mechanical stimulation of the anterior surface of *Paramecium* induces a mechanosensitive depolarising potential. In wild type cells a regenerative calcium action potential causing ciliary reversal is always accompanied by the anterior mechanoreceptor potential, caused by an increase in Ca^{2+} permeability after mechanical stimulation^{12,13}. The responses of the proboscis surface of hungry *Didinium* to mechanical stimulation and that of the proboscis of fed *Didinium* to collision with a *Paramecium* are similar to the above responses of *Paramecium*.

The *Paramecium*-sensitive hyperpolarising potential and the depolarising action potential associated with discharge of the extrusive organelles were characteristic features of the prey capture behaviour of *Didinium*. The action potential was always

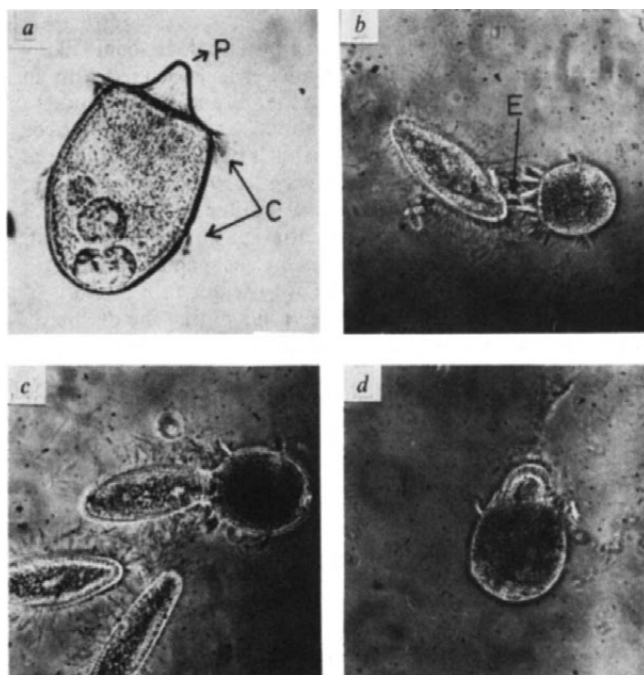


Fig. 1 Hungry *Didinium* (a), and successive phases of the capture and ingestion of *P. caudatum* by *Didinium nasutum* (b, c and d). Photographed under interference-contrast illumination. (a, $\times 100$; b, c and d, $\times 50$.) P, proboscis; C, cilia; EO, extrusive organelles.

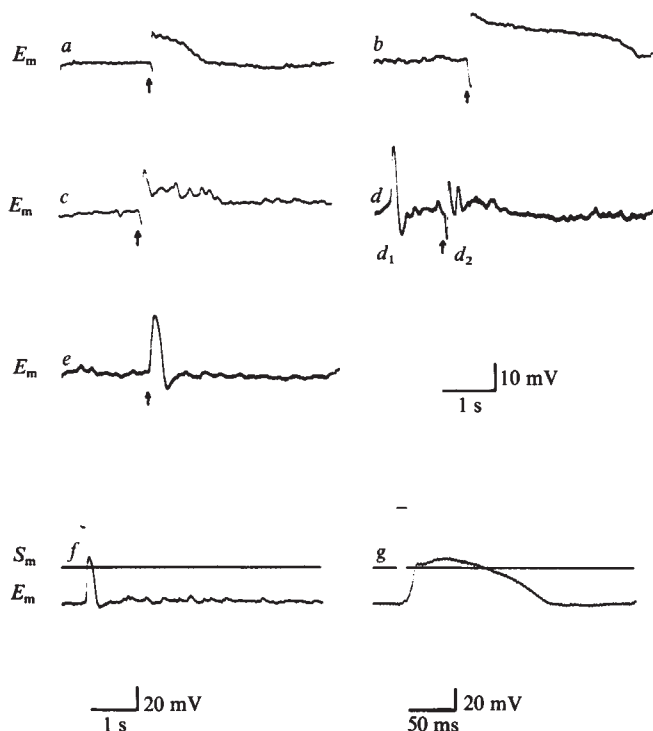


Fig. 2 Responses of the membrane potential to collision between *P. caudatum* and the apex of the proboscis of *Didinium nasutum* (a, b, c, d₂ and e). Arrows show the moment at which a *Paramecium* collided with the apex of the proboscis of *Didinium*. Spontaneous ciliary reversal response is also shown (d₁), together with responses to mechanical stimulation of the apex of the proboscis (f and g). a, b, c, d, f and g, hungry *Didinium*; e, fed *Didinium*. E_m, membrane potential; upward and downward deflections correspond to depolarisation and hyperpolarisation of the membrane, respectively. S_m, deflection in the trace indicates the duration and relative intensity of the electric pulse activating a piezoelectric crystal to drive a glass rod against the surface of the membrane. Membrane potentials were recorded in mixtures of 1 mM K⁺, 1 mM Ca²⁺ and 1 mM Tris-maleate (pH 7.0) (a, b, c, d and e) and 1 mM K⁺, 1 mM Ca²⁺ and 1 mM Tris-HCl (pH 7.2) (f and g). All measurements were made at room temperature (20–25°C).

accompanied by the hyperpolarising potential. It seems likely that the discharge of extrusive organelles is associated with an inflow of Ca²⁺ through the proboscis membrane due to a sudden increase in Ca²⁺ permeability, enabling Ca²⁺ to flow inwards down its electrochemical gradient. This is because the discharge of extrusive organelles was always associated with the depolarising action potential, which was different from a general membrane depolarising action potential causing ciliary reversal, and membrane depolarisation in this species seems to involve an inflow of Ca²⁺, as in the case of *Paramecium* in a mixture of 1 mM K⁺ and 1 mM Ca²⁺. It has been shown that the discharge of *Paramecium* trichocysts is associated with a flow of Ca²⁺ through the membrane¹⁴.

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Estimation of cytoplasmic and vacuolar pH in higher plant cells by ³¹P NMR

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It has recently been emphasised that the intracellular pH of plant cells must be actively regulated to offset acid-base imbalances that occur during metabolism and solute uptake (for review see ref. 1). Changes in cytoplasmic pH might be important (1) in controlling various aspects of metabolism², including enzyme activities responsible for malate synthesis during cation accumulation^{1,2}, (2) in polar transport of the plant hormone, auxin³, and (3) in intracellular responses to substances such as auxin and the phytotoxin fusaric acid, which cause proton extrusion^{1,4,5}. Almost no direct measurements of cytoplasmic pH have been made on the small cells typical of higher plants¹. The task is hampered by the presence of a generally acidic vacuole which occupies much of the cell volume. Use of the indirect method of ¹⁴C-5, 5-dimethylxazolidine-2, 4-dione (DMO) distribution is subject to considerable uncertainties because of corrections needed for vacuolar pH and volume, and DMO metabolism^{6,7}. Here we report the use of ³¹P nuclear magnetic resonance (NMR) to estimate the pH of vacuole and cytoplasm in maize root tips.

The observation of intracellular organic and inorganic phosphates by ³¹P NMR has been proposed as a method for determining the internal pH of animal and microbial cells^{8,9}. As the chemical shift (δ, the resonance frequency relative to a standard) of ³¹P in these compounds yields a titration curve when plotted against pH (insert in Fig. 1), a determination of pH from a measured δ value is possible in principle. The advantage of the method is that it is noninvasive and nondestructive. The principal problem in its use is that pH may be the dominant, but is not the sole determinant, of δ. However, the resulting ambiguities are not severe, as will be discussed below.

Figure 1a shows a typical ³¹P-NMR spectrum of maize root tips showing resonances from glucose-6-phosphate (G-6-P, peak 1) and inorganic phosphate (P_i, peaks 2 and 3). The

Table 1 ³¹P-Chemical shifts observed in maize root tips, and corresponding pH values

Treatment	δ (p.p.m.) of peak relative to MDP			Corresponding pH values		
	1	2	3	1	2	3
Control	12.6	14.7	16.4	7.25	7.15	5.5
Control	12.65	14.7	16.4	7.1	7.15	5.5
Control	12.6	14.75	16.4	7.25	7.05	5.5
2-dG*	12.68	—	16.45	7.2	—	5.4
6 mM NH ₄ OH†	12.58	14.6	16.0	7.3	7.2	6.05
12 mM NH ₄ OH†	12.55	14.55	15.6	7.4	7.3	6.4

Control root tips were prepared and treated as for Fig. 1a. Columns headed 1, 2 and 3 refer to NMR peaks 1, 2 and 3 illustrated in the Figs 1 and 2.

* Root tips were incubated for 2 h in 50 mM 2-dG at 23°C. pH value given for peak 1 is based on the titration curve of 2-dG-6-phosphate. Peak 2 was too small to be assigned a δ value in 2-dG-treated tissue.

† Root tips were incubated in 10 ml of 6 or 12 mM NH₄OH (initial pH 9.6) at 23°C for 30 min (final pH 6.56 and 7.2, respectively).

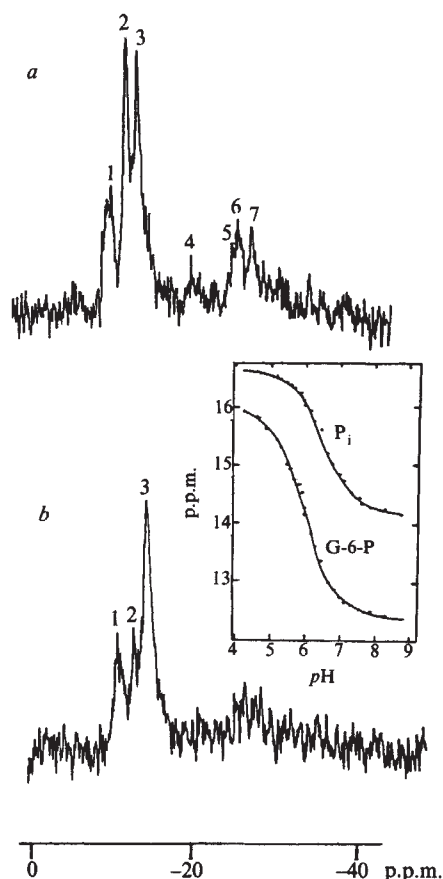


Fig. 1 *a*, 145.7 MHz ^{31}P -NMR spectrum of maize root tips (~ 900 tips or ~ 1.2 g) 1.5 mm long. Maize (*Zea mays* L.) WF9 $\times$ Bear 38 were soaked for 6 h in tap water, and grown for 2 days on moist tissue in the dark, at 25 $^{\circ}\text{C}$. Plants were collected in the light, root tips 2–3 mm long being excised with a razor blade, and then put on ice. Before being placed in the NMR tube, they were washed three times with ice-cold distilled water. (Washing with 1 mM EDTA did not affect the quality of the spectra obtained.) Spectra were obtained at 5 $^{\circ}\text{C}$ with ~ 400 scans at 0.409 s per scan without proton irradiation and without lock using a modified Bruker HXS-360 spectrometer. Shifts are referenced to 0.05 M methylene diphosphonic acid (MDP) in pH 8.9 Tris buffer, located in a coaxial capillary tube. *b*, Spectrum of root tips 2.5 mm long, grown and prepared as *a*. Peak 1, G-6-P; 2, cytoplasmic P_i ; 3, vacuolar P_i ; 4 and 5, ATP; 6 and 7, UDP-Glc.

individual peaks can be identified on the basis of the relative chemical shifts and the published analyses of phosphate compounds in growing plant tissues^{10–13}. Enzymatic analysis¹⁴ of maize root tip perchloric extracts confirms that G-6-P is the predominant hexose phosphate.

The resonance due to G-6-P in maize root tips has a δ value corresponding to pH 7.1–7.25 (Table 1). Because G-6-P is an important cytoplasmic metabolite, and is not considered to form a significant storage pool, the G-6-P resonance probably reflects the pH of the cytoplasm. The positions of the two clearly resolvable peaks in the P_i region of the spectrum correspond to P_i at pH 7.05–7.15 (peak 2) and pH 5.5 (peak 3). This suggests that we are detecting resonances from two separate compartments in these cells—cytoplasm (pH ~ 7.1) and vacuole (pH ~ 5.5). These inferences are supported by the following observations:

(1) A spectrum (Fig. 1*b*) obtained from longer root segments, which contain much more highly vacuolate cells, shows much smaller peaks 1 (G-6-P) and 2 (cytoplasmic P_i), relative to peak 3 (vacuolar P_i), than are seen in root tips (Fig. 1*a*), the cells of which contain relatively more cytoplasm. In the more vacuolate tissue (Fig. 1*b*) the peaks corresponding to other important ^{31}P -containing cytoplasmic metabolites (ATP, UDP-Glc) are also reduced. A highly vacuolate tissue, such as the coleoptile of

maize, yields only one ^{31}P resonance, corresponding to P_i at pH 5.5, that is, peak 3 (data not shown).

(2) When a root tip sample is aged at ~ 5 $^{\circ}\text{C}$ for 2–3 h in a closed (and thus anaerobic) NMR tube, peak 1 (G-6-P) decreases and peak 2 (cytoplasmic P_i) increases correspondingly, without much change in peak 3 (vacuolar P_i) (Fig. 2*a, b*). This presumably reflects depletion of G-6-P, as is known to occur in conditions of oxygen starvation^{10,11}, with release of P_i but without loss of the normal compartmentation of the cells. When tissue is similarly aged for 7–8 h the G-6-P peak disappears entirely, and the two P_i peaks (2 and 3) merge into a single peak that has a δ value intermediate between the two (not shown). This is to be expected as the cell die and their internal compartmentation breaks down.

(3) If root tips are incubated with 2-deoxyglucose (2-dG), a large ^{31}P resonance in the sugar-phosphate region appears (Fig. 2*c*). This peak can be attributed to 2-dG-6-phosphate, the principal metabolite formed when cells take up 2-dG^{15,16}. Concomitantly, peak 2 (cytoplasmic P_i) virtually disappears, whereas peak 3 (vacuolar P_i) remains strong. This corresponds with the expectation that cytoplasmic P_i will be used to phosphorylate 2-dG in the cytoplasm, where hexokinase is located.

(4) When root tips are incubated in dilute solutions of the permeant base, ammonia, the δ values of peaks 1 and 2 show little change, whereas that of peak 3 changes substantially,

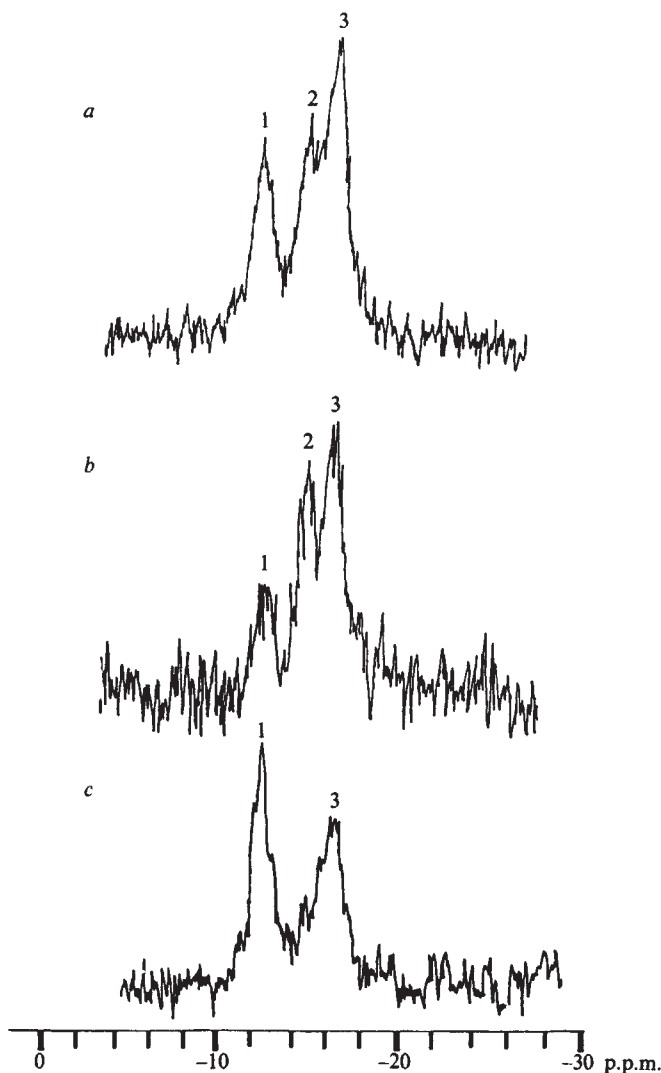


Fig. 2 ^{31}P -NMR spectra obtained from: *a*, maize root tips prepared as in Fig. 1*a*. *b*, The same root tips sample as in *a* after 2 h at 0–5 $^{\circ}\text{C}$ in the NMR tube; peaks 1, 2 and 3 as in Fig. 1*a*. *c*, Root tips that had been incubated in 50 mM 2-dG for 2 h at 23 $^{\circ}\text{C}$; peaks 1, 2-dG-6-phosphate; 3, vacuolar P_i .

corresponding to a substantial rise in pH (Table 1). This suggests again that peaks 1 and 2 are due to ^{31}P in one compartment, peak 3 to ^{31}P in a different compartment. These results also indicate, as might be expected¹, that the cytoplasmic pH of these cells is regulated much more closely than that of the vacuole.

The pH values reported here should be regarded as approximate because the relationship between the δ values of ^{31}P compounds, and the pH as measured with a glass electrode, can differ in media of different composition. Although it has been reported⁹ that Mg^{2+} has no effect on the titration curve of P_i , we find that both Mg^{2+} and concentrated protein shift the apparent pK_a of P_i and G-6-P to a lower value, by as much as 0.2–0.4 pH units. These effects will be described in detail elsewhere. The difference in apparent pH between the two compartments detectable by NMR in this tissue is, however, much larger than could be caused by known perturbations of the ^{31}P compounds. The ^{31}P method can therefore be useful for testing whether intracellular pH changes during certain physiological responses¹.

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Table 1 The enhanced effect of cyclic AMP and diuretic hormone stimulation after L-canavanine treatment

Response to:	% Increase in rate of fluid secretion	
	s Control tubule	Canavanine-treated tubules
Cyclic AMP (10^{-3} M)	61.79 $\pm$ 5.90 ($n = 13$)	764.18 $\pm$ 45.81 ($n = 11$)
Diuretic hormone (5 pairs storage lobes)	88.83 $\pm$ 8.41 ($n = 10$)	339.99 $\pm$ 50.25 ($n = 9$)

Values are means $\pm$ s.e.m.

In contrast to mammals, insects do not possess a closed, high blood pressure circulatory system. Therefore they lack the initial force present in the mammalian kidney which is responsible for the formation of a primary urine filtrate. They rely primarily on a diuretic hormone for the production of a rapid flow of fluid through the tubules. The response to diuretic hormone is dramatic in blood-sucking insects that feed infrequently⁸. Between feedings they carefully guard their water loss but on feeding they imbibe vast quantities of fluid relative to their size, and the surplus water is then rapidly excreted. The *in vitro* response to exogenous diuretic hormone or to exogenous cyclic AMP is far less striking in plant-feeding insects, such as locusts, that feed regularly. Presumably their malpighian tubules are already somewhat stimulated and the increase in secretion as a consequence of their exposure to diuretic hormone or to cyclic AMP, is limited. Most of the insect's body fluid is circulated through the excretory system in a short span of time² and derangement of the orderly process of events could rapidly lead to fatal dehydration^{4,5}. This is what happens when L-canavanine⁴ or other non-protein amino acids⁵ are injected into the haemolymph of the insect. On the other hand when insects are exposed to chronic doses of L-canavanine by feeding³ death is due to the retention of water. It is clear that such apparent contradictions need resolving.

Malpighian tubules of locusts were isolated according to the method reported previously⁹. This involved the removal of the whole length of the gut with the tubules attached. The gut was bathed by a physiological saline medium in a wax-bottomed Petri dish and the whole preparation was maintained under liquid paraffin. The tubules were cut at their entrance into the gut and the cut end was extended around fine glass rods held by the wax. Drops of secreted fluid thus formed at the cut end and were subsequently measured.

Tubules were incubated in bathing media until basal secretory rates stabilised. Bathing media were subsequently changed to those containing L-canavanine, at a concentration of 10^{-4} M and secretory rates were monitored. The results are shown in Fig. 1 and compared to the performance of the tubules in normal *in*

Canavanine potentiates the response of insect malpighian tubules to diuretic hormone and cyclic AMP

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Insects regulate the amount of water they excrete via their malpighian tubules, the degree of stringency depending on the hydration of their diet and on the frequency at which they feed. The excretion of water is controlled by a diuretic hormone, which is released as required into the haemolymph by the corpora cardiaca^{1,2}. Previous reports^{3–5} have shown that non-protein amino acids, known to be neurotoxic in vertebrates⁶ as well as in insects⁷, lead to a disruption of water balance in insects. However, the exact mode of action of these amino acids has not been elucidated. We report here on preliminary experiments using isolated malpighian tubules of locusts *Locusta migratoria migratorioides* (R & F) which show that the non-protein amino acid L-canavanine inhibits fluid secretion *in vitro* by isolated tubules. Furthermore, when tubules, previously inhibited by canavanine, are subsequently stimulated by exogenous diuretic hormone (methanol extracts of storage lobes of corpora cardiaca^{1,2}) or cyclic AMP (which mimics the action of diuretic hormone¹), the stimulation obtained is much greater than that normally expected from diuretic hormone or cyclic AMP.

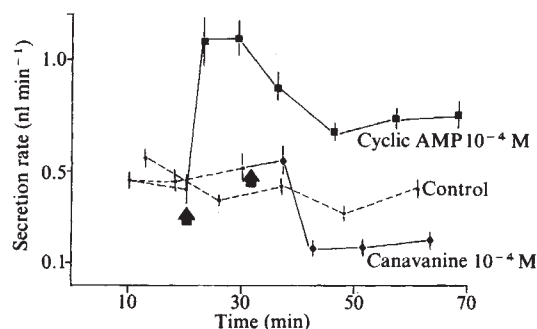


Fig. 1. The effect of L-canavanine and cyclic AMP on the malpighian tubules of *Locusta*. Arrows indicate time of administration of test substance. Number of observations in all cases is 10.

vitro conditions and on addition of bathing media containing cyclic AMP. After 7 min of canavanine administration the rate of fluid secreted by the tubules drops by 72.7%. After this initial drop the fluid rate stabilises to a new basal level much lower than the normal original level. On the other hand, cyclic AMP stimulates fluid secretion almost immediately (3 min after administration) and the rate stabilises to a new basal level, higher than the normal original level. Inhibition is also evident when both cyclic AMP and canavanine are administered together in the bathing medium (Fig. 2). The cyclic AMP dose-response curve drops significantly when canavanine is present showing a substantial inhibition of tubular fluid secretion (32.6% inhibition at 10^{-3} M cyclic AMP).

In an attempt to determine whether canavanine inhibition is reversible, experiments were designed in which cyclic AMP was added to the bathing medium after treatment with canavanine. It was found that the tubules not only responded to the stimulatory effect of cyclic AMP but their response was enhanced to a remarkable extent (>700% increase in rate) when compared to the normal response of untreated tubules (Table 1). Since cyclic AMP mimics the action of the naturally occurring diuretic hormone¹, we tested the response of the tubules to diuretic hormone in canavanine-treated and untreated tubules (Table 1).

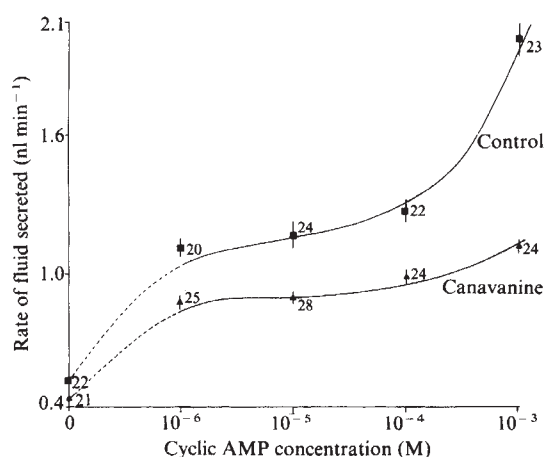


Fig. 2 The effect of L-canavanine on the normal dose-response curve of cyclic AMP. Subscript numbers indicate number of observations. Curves were fitted by eye.

It is clear that the diuretic hormone similarly stimulates canavanine-treated tubules to a greater extent (>300% increase in rate) than untreated tubules. Thus canavanine, although in itself inhibitory, influences the tubules to react to a stimulatory compound much more effectively, possibly to the detriment of the insect.

We are now in a position to explain the apparent contradiction between the response of the whole organism to chronic exposure of canavanine (seen as a marked retention of water) and to a sequential exposure (seen as a loss of body fluid and dehydration). The inhibition of the isolated malpighian tubule by canavanine would lead to a marked retention of water. This is consistent with the retention of water which occurs *in vivo* in conditions of chronic exposure³. Since tubules themselves are capable of inactivating diuretic hormone¹⁰, we assume that the inhibitor effect of canavanine occurs at a time when levels of endogenous diuretic hormone are much reduced. Canavanine apparently primes the tubules to respond to subsequent influx of diuretic hormone or to the generation of cyclic AMP. Indeed, the addition of diuretic hormone or cyclic AMP to tubules inhibited by canavanine elicits a dramatic increase in fluid transport, consistent with the dehydrated state attained *in vivo*^{4,5}. This would only be true if exposure to canavanine is for a limited period which occurs when canavanine is administered by

injection. Whether this priming is due to a general alteration in membrane transport properties is not yet clear.

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Use of cellulase antibodies to study leaf abscission

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The primary leaves of the bean (*Phaseolus vulgaris* c.v. red kidney) are shed as the result of cell wall breakdown in the abscission zones found at the base of the lamina and at the stem-petiole junction. Horton and Osborne¹ suggested that cellulase (B 1:4 glucan 4-glucanohydrolase) was involved in this wall hydrolysis because its activity increased considerably during abscission. Although this result has been repeated on a wide range of plant material², critical scrutiny of the data has led several authors^{3,4} to question the direct involvement of the enzyme in wall weakening. The following objections have been raised: (1) cellulase may be present at relatively high levels before abscission is induced⁵, (2) although wall breakdown is confined to two or three layers of cells, cellulase is usually found over a wider area of the petiole, (3) the increase in cellulase which accompanies abscission may not take place until cell separation is essentially complete³, (4) cellulase may increase without concomitant breakdown of the abscission layer⁴. One possible explanation for these anomalies is that these assays failed to distinguish between the various isozymes of cellulase, of which only one is postulated to be involved in abscission⁶. Recently, the specific isozyme thought to participate in bean leaf abscission (9.5 cellulase) has been purified and monospecific rabbit antibodies raised against it⁷. These antibodies do not cross-react with the other form(s) of cellulase and thus can be used both to quantify changes in 9.5 cellulase during abscission and to determine cytochemically the distribution of the enzyme. Using these antibodies, we have now made observations consistent with the participation of cellulase in the wall hydrolysis which leads to fracture.

Figure 1 shows a typical time course of abscission. At the time of induction the levels of total cellulase in the abscission zone can be easily detected. These increase dramatically after 18 h, when the force necessary to break the abscission zone declines. If the 9.5 isozyme is distinguished by radioimmune assay it is virtually undetectable in the uninduced tissue but starts to rise at 18 h just before a decrease in strength of the abscission zone. The correlation between the rise in 9.5 cellulase and the decrease in break strength is striking.

The antibody has also been used to localise the enzyme in formaldehyde-fixed cryostat sections (Fig. 2). This method reveals that 9.5 cellulase is confined to the two or three rows of

cortical cells through which the fracture will pass and is also found in a wide band of vascular tissue. Unfortunately, nonspecific binding of antibody to the vascular tissue made interpretation of this observation difficult. To check these localisations, small fragments of tissue (100 μ g) were dissected from the cortical and vascular areas of the fracture face and the cellulase content compared with adjacent areas outside the abscission zone. The stele contained very high levels of cellulase (2,012 units per g) in the zone compared with the vascular trace proximal to it (31 units per g). The abscission zone cortex also had elevated levels (167 units per g) compared with the general petiolar cortex (14 units per g). These viscometric assays are thus consistent with the immunocytochemical staining patterns showing 9.5 cellulase to be restricted to the fracture plane in the cortex. In the vascular tissue, cellulase is not limited to such a precise band of cells; this may account for the rather variable line of fracture in this tissue and objection (2) above.

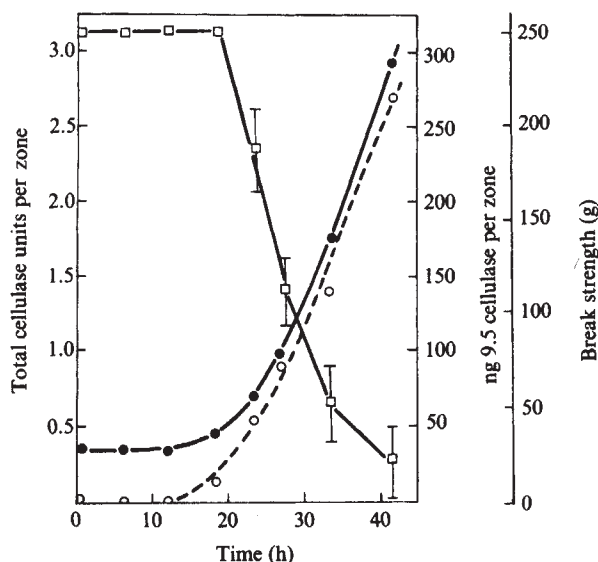


Fig. 1 A time course of abscission in the stem-petiole abscission zone of primary bean leaves. Eleven-day-old plants were induced to abscise by deblading 2.5 cm above the stem-petiole junction. The explants were placed in a chamber through which 50 p.p.m. ethylene was passed (1 l min⁻¹) in CO₂-free air. Samples of 70 zones were taken at the time points shown and the break-strength or force necessary to fracture the abscission zone determined⁵ (□). Also, at each time point 70 zones were excised, extracted in salt-fortified buffer and total cellulase determined by a viscometric assay according to the methods of Lewis and Varner⁵ (●). Radioimmuno assay was carried out on the same samples (○). 9.5 Cellulase purified by the methods of Koehler *et al.*⁷ was iodinated with ¹²⁵I using the chloramine T method essentially as described by Chard⁸. The iodinated cellulase was separated from its contaminants by chromatography on a cellulose column and elution by cellobiose⁷. The construction of a calibration curve and determination of unknown samples were carried out as described by Chard⁸. Results are all expressed on a per zone basis.

Thus, both the time course of 9.5 cellulase appearance and its distribution are completely consistent with an involvement in abscission. In an attempt to substantiate this role further, we injected serum containing 9.5 cellulase antibodies into the laminar abscission zone. It was hoped that the antibody would reach the exocellular cellulase producing the precipitin complex and so preventing its active involvement in wall hydrolysis. Two batches of 250 laminar abscission zones were injected with either 2 μ l of normal rabbit serum or serum containing 9.5 cellulase antibodies (titre 4,900 units ml⁻¹). This was achieved by passing the needle of a 'Hamilton' syringe along the centre of the petiolar pith cavity until the resistance of the pulvinus was

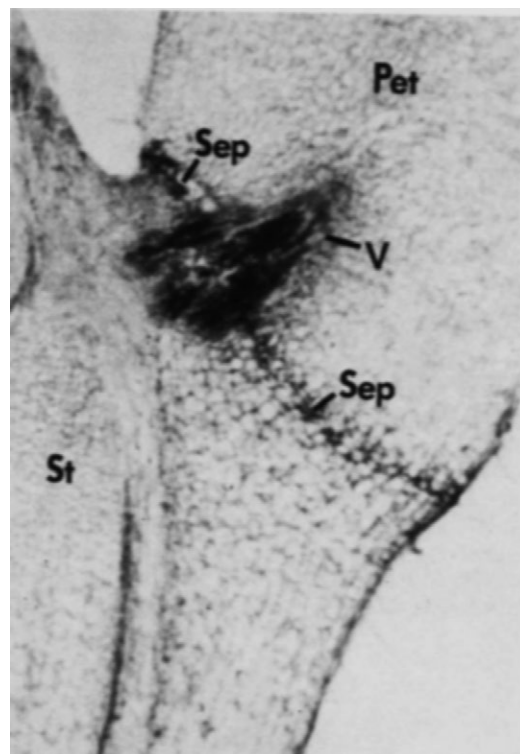


Fig. 2 A longitudinal cryostat section through the petiole base 36 h after the induction of abscission, incubated to show the distribution of cellulase. The enzyme was localised using the indirect method. Formaldehyde-fixed sections were placed first in rabbit anti-cellulase serum. After washing and denaturation of the native peroxidase⁹, they were placed in diluted peroxidase-conjugated goat anti-rabbit immunoglobulin G. After further extensive washing, the bound peroxidase was localised by Graham and Karnovsky's method¹⁰. St, stem; Pet, petiole; Sep, separation layer; V, vascular trace. $\times 25$.

met. At this point, the needle tip rests in the fracture plane in the vascular area where most cellulase is produced. Injections were made at 6-h intervals during the period when the 9.5 isozyme appeared, and then at 40 h the break strengths of the zones were determined. The zones injected with normal serum had an average break strength of 49 g (± 26.1 g) whereas 90% of those treated with cellulase antiserum failed to break even if 200 g was applied. The 10% of this sample which did break in the abscission plane had mean break strengths of 167 g (± 20.4 g). Thus, the injection of 9.5 cellulase antiserum had almost completely prevented wall breakdown. The levels of cellulase recovered from these cellulase antibody-treated zones was 24.4% of that in the normal serum controls. Presumably, this represents the enzyme which was inaccessible to the antibody, perhaps at intercellular sites in the tissue. As the antiserum has been proved to be specific to 9.5 cellulase⁷, the fact that it stops abscission while the normal serum does not, confirms that cellulase has a central role in the abscission process.

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STUDENT BOOKS SUPPLEMENT

The lives of the spineless

H.C. Bennet-Clark

THE teaching of the zoology of invertebrates, like their classification, has been the subject of the changing fashion. Major pedagogic problems are whether to lay emphasis on systematics or on comparative functional biology, whether to underpin the subject with comparative anatomy or with arguments about phylogeny. The subject is so vast and has such an extensive literature that any attempt to present, in a single textbook, a comprehensive account of the invertebrates is bound to be unbalanced and incomplete; one must therefore judge any text on the insight it shows and on the impact it will have on students of all ranges of interest and ability. Here, at once, we have three very different approaches, none exhaustive but all with contrasting merits.

The easiest to evaluate, because its aims are the least controversial, is Laverack and Dando's *Lecture Notes on Invertebrate Zoology*, now in a somewhat enlarged and welcome second edition. As the title implies, the work offers a series of brief descriptions of all invertebrate phyla, giving a diagnosis and brief description of the anatomy, aspects of the physiology, development and classification of each phylum.

For small groups such as the Echiura or Brachiopoda, this formula works well enough, though the former are described within the chapter as both Echiurids and Echiurida; and for the latter there is neither a description of the structure and composition of their shells, nor of their embryology nor, possibly wisely, a discussion of their affinities.

With the larger phyla, notably the Protozoa, Arthropoda and Mollusca, the treatment becomes less successful. That of the Protozoa, compressed into 11 pages, is so brief as to be confusing, while for the Mollusca a similar compression leads to over-brief treatment of the major classes Gastropoda and Lamellibranchia (surely Bivalvia?). With the Arthropoda the problems seem more deeply rooted. I find it

Lecture Notes on Invertebrate Zoology. Second edition. By M.S. Laverack and J. Dando. Pp.194. (Blackwell Scientific: Oxford, 1979.) Paperback £5.50. *A Life of Invertebrates*. By W.D. Russell-Hunter. Pp.650. (Collier-Macmillan: West Drayton, UK, 1979.) £12.75. *The Invertebrates*. By R. McNeill Alexander. Pp.562. (Cambridge University Press: Cambridge and New York, 1979.) Hardback £28; paperback £7.95.



hard to equate the larval forms and metamorphoses of Crustacea with those of Insecta and so I am unhappy to see these described together. Whatever one's views of the controversy, one cannot reasonably ignore the work of S.M. Manton on Arthropod phylogeny; but there is no discussion either of this or of the relations

between the major Arthropod taxa.

On the whole this is a useful book. The pictures are borrowed but plentiful and well chosen, there are brief but handy lists of references — with notable omissions of some major works published in the last couple of years; the layout is good and the price is right.

Russell-Hunter's *Biology of Lower and of Higher Invertebrates* are old friends and deserved the success they achieved. Published about ten years ago, they now creak a little so this, their derivative, *A Life of Invertebrates*, is timely. The formula is similar; a series of chapters on aspects of the biology of different phyla — a couple on the Coelenterates, a couple on Crustacea, eight on Mollusca, one into which "Walking Worms" (Ugh! — guess the phylum), the Tardigrada, Linguatulida and Echiuroidea (!) are concreted. Between and within these are useful chapters, sadly under-played in the other texts: on metamerism in the Annelida; on the super phyla of the animal kingdom; on the phylogeny of the invertebrates; and so on.

At points the layout and balance are slightly suspect. Protozoa are considered in a single brief chapter and after the Coelenterates, which receive three chapters. The insects are skimmed in a single chapter and in rather less detail than the treatment accorded to gastropod or cephalopod molluscs. Against this, the text is mostly well laid out, written and illustrated; and, above all, the author manages to convey an admirable feel for particular phyla without congesting his text with turgid and repetitive detail.

Even though it is so clearly presented, I have reservations about this book, even as the elementary text it is designed to be. I find many of the diagrams — such as those of the tunicates (32-2) or of the tardigrade (18-2) — too sketchy, though other original diagrams are excellent. I cannot but contrast the clarity of Russell-Hunter's exposition on worm locomotion with his

excessively thin description of protozoan locomotion, a topic which Alexander handles lucidly and in detail. Above all, I find it hard to recommend to my students any text from which access to primary sources is so difficult. True, there is an annotated bibliography at the end of the book but exclusively to textbooks. It would, for example, be hard to discover details of the functioning of crustacean endocrine systems or of the lamellibranch filter-feeding gill from any of the sources he cites, even though both topics are described by him in considerable detail.

In Alexander's *The Invertebrates*, there is no attempt to describe the diversity of major morphological characteristics of invertebrate phyla and, in his preface, Alexander writes: "This sort of information is available in existing textbooks and indeed dominates some of them so that they fail to reflect current trends in zoology". Those who know and respect his other books will expect to be enlightened and excited by his latest offering — and will not be disappointed.

Here are many insights into the operation of invertebrates; I have only space to select a few titbits. The description of how a flagellum works, though simplified, is up-to-date, rigorous and

understandable. It extends to a comparison of forms in which the direction of swimming is the same as that of the flagellar beat with those in which they are opposite. There is also a nice comparison of the roles of geodesic fibres in different phyla — in nemerteans as constraints on both the maximum and minimum length obtainable, in nematodes as antagonists to the longitudinal muscles, and in the mantles of cephalopods as constraints on the length during jet propulsion; the first two, of course, are well known but it is nice to see the story extended and elaborated. The shells of molluscs are treated both as geometrical structures and as examples of skeletal materials. Where, in these descriptions, a series of calculations is required to substantiate the argument, the reader is led through a gentle series of 'O' level sums!

As Alexander is scrupulous in referring to his sources in text, in figure legends and in generous chapter bibliographies, it is easy to pursue topics further. But woe betide the student who, buying this book, expects to master the invertebrates. He will not find much on the systematics or relations between invertebrate groups and only an occasional and often highly specific account of anatomical features. It must

therefore, to achieve its aims, be used in conjunction with more solid conventional text books.

I find the book enthralling and irritating. Enthralling because of the insights that are offered and the novelty of the approach. Irritating because it treats the different invertebrate phyla in an inconsistent rather patchy way, because the student may be seduced into believing that comparative systematics and anatomy may be ignored and, rather pettily, because many aspects of invertebrate biology that I had laboriously collected to gild the unleavened gingerbread of my teaching are here gathered together, augmented, under one cover. As a text, it may not endure but it will certainly be influential and is a 'must' in any reading list.

These are three very different treatments. All offer a welcome relief from the larger 'straight' invertebrate zoology textbooks. None, alas, is sufficiently comprehensive to stand on its own. Equally, each has its considerable merits and a place in any course in invertebrate zoology. □

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Parasitological literature

R.W. Ashford

Medical Parasitology. By R. Leventhal and R.F. Cheadle. Pp.168. (F.A. Davis: Philadelphia, 1979.) \$19.95. *Parasites and Western Man*. Edited by R.J. Donaldson. Pp.220. (University Park Press: Baltimore, 1979.) £12.95. *The Biology of Parasitism*. By P.J. Whitfield. Pp.277. (Edward Arnold: London, 1979.) Paperback £7.95.

PARASITOLOGY may be approached as an applied or academic subject, and the applied subject requires workers at all levels of sophistication. These three books span the field: an elementary practical text; a more specialised applied text; and a strictly academic volume in which apology is made for dealing in detail with those applied aspects which have contributed to understanding.

The self-instructional text by Leventhal and Cheadle is aimed at students of laboratory technology, medicine and biology. This volume differs from many works by including short-answer self-assessments at the beginning of the book and at the end of each chapter, and a final

examination at the end of the book. The text describes the main parasites of man, using verbal rather than graphic life cycle diagrams, tables, diagrams of the diagnostic stage, and glossaries of terms. A section deals with laboratory techniques. Finally there is a collection of colour photographs illustrating many of the parasites. Although the book was evidently produced hurriedly, as indicated by the many typographical errors, much of the information and terminology is out-dated. The colour photographs do not bear comparison with those in a number of readily available books; they are sometimes strangely coloured, and the inaccuracy of some of the magnification scales will make them of little help in identifying real parasites.

A concise text with test questions could have been a useful aid to revision for examinations; it is unfortunate that this volume fails to meet the required standard.

Parasites and Western Man, produced by a team of eminent contributors, is aimed at medical and veterinary workers at all levels, particularly those with public health interests. In materially advanced Western society much of the public health problem concerns imported infection, but there are also surprisingly large numbers of parasites which hang on, and even thrive, in Western countries. In his introductory chapter, Nelson, provocative as ever, expounds the argument that parasites may have a positive role in human health, and that the search for a balanced relationship with

them may be more valuable than blind destruction.

Each major group of parasites is covered in a chapter, and the ubiquitous head lice are given one of their own. Concluding chapters deal with the role of pets and domestic animals in human parasitic infections. The life cycles, modes of transmission, clinical and public health aspects, and statistics of occurrence of parasites in Western countries are outlined; and in the case of the more prevalent lice and mites, considerable epidemiological detail is given. More of this detail would have been useful for other parasites.

If this work has a wide enough circulation, it may help to control both the irrational horror which attends the discovery of a louse or pin-worm, and the equanimity with which the pollution of our residential areas by faeces from pet animals is commonly viewed. Despite a few slips, and the repetition inevitable in a multi-author work, this is a highly readable, thoroughly authoritative text which fills a gap in the literature.

Whitfield's *Biology of Parasitism* is a brave effort to summarise, for undergraduate and early postgraduate biologists, the outcome of technological and conceptual advances in the subject over the last ten years. The treatment of the whole subject of "Association Biology" in a "unified" language has allowed a broader view than is customary. Structure, nutrition, physiology, behaviour and ecology are reviewed in separate chapters.

The impressive breadth of subject covered has meant that depth has been limited; instead of indulging in broad generalisations, however, the author has achieved this by concentrating in depth on a few well-worked examples. In many cases a single association is viewed from different aspects in different chapters, and this gives continuity to a work which could easily have become disjointed. Recent information on surface interactions between parasites and hosts is covered in detail, and though the whole subject of parasite immunology is reduced to thirteen pages, the latest advances are summarised without gross oversimplification. The section on population studies is notable for the contribution which the author and his colleagues have made, but there remains an important communication gap between applied epidemiologists and the theoretical ecologists.

There is no attempt to be comprehensive or to supersede existing textbooks; this is a complementary work for advanced students. It will be particularly valuable as a basis for seminar discussions and as a source of wide-ranging up-to-date references. My only complaint is that the fashionable complexity of the language used, though meticulously accurate, will preclude the use of this book by many overseas students.

Three contributions to the sagging shelves of parasitological literature: our students, on appropriate courses, will be advised to avoid Leventhal and Cheadle, to at least read Donaldson, and to buy Whitfield. □

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Radioactivity in context

Malcolm C. Scott

Radioactivity: A Science in Its Historical and Social Context. By E.N. Jenkins. Second edition. Pp.197. (Taylor and Francis: Basingstoke, UK, 1979.) Paperback £4.75.

THE discovery of radioactivity and, subsequently, fission is one of the many fascinating stories associated with the development of science generally, and one which gives as valuable an insight as any into the nature of the scientific method. The general topic of radioactivity and its exploitation is also one for which it can be argued that there are moral issues involved, principally in the use of nuclear power. A book covering both these aspects should, therefore, provide stimulating reading.

It is therefore with regret that one records that the author of this book has not been able to meet the challenges presented in communicating either the excitement of discovery or the moral implications. Although the thirteen chapters cover a reasonably comprehensive spread of material, ranging from 'The Discovery of Radioactivity' through 'The Chemistry of the Fission Products' to 'The Biological Effects of Radiation', the quality of the coverage is not very uniform. As the author was a research chemist until taking holy orders in 1962 it is perhaps to be expected that the chemistry sections are the most fluent. However, some of the other sections seem disjointed and even faintly dated, in the sense that developments since the book's first edition, in 1962, sometimes do not get the weight which workers active in the field would assign to them.

Additionally, the advances made in the teaching and textbook presentation of scientific material in the 1960s and 70s are not reflected here: in fact, parts of the book are distinctly heavy going, and would hardly seem to appeal to the first-year university student, or equivalent, for whom the book is intended.

There are a number of minor errors and misleading statements which, though not central to understanding, leave one uneasy. For example, the different quenching mechanisms in a Geiger counter are confused (page 24) and the definition of neutron multiplication factor (page 107) cannot easily be related to and is inconsistent with the data given in the associated table. Perhaps the most disappointing aspect, however, is that moral and social questions do not get the depth of coverage which one would expect from reading the introduction. For example, what does the risks versus benefit balance sheet look like for the medical uses of radiation or for nuclear power? Are enough facts known for us to be able to draw up such a balance sheet? Can there be a qualitative difference between risks producing the same number of deaths in a given period of time and, related to this, what makes some risks socially acceptable whilst other, lower ones, are unacceptable? The reader looking for a discussion of these and related questions will not find them, yet these, surely, lie at the heart of any 'moral' evaluation.

Given the didactic philosophy behind the *Wykeham Science Series* and the excellence of some of the resulting books this one is somewhat disappointing. □

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Behaviour of practical systems

I.S. Grant

Transmission and Propagation of Electromagnetic Waves. By K.F. Sander and G.A.L. Reed. Pp.410. (Cambridge University Press: Cambridge and New York, 1978.) Hardback £24.50; paperback £5.95.

THIS book is intended to be used as a textbook in the later stages of undergraduate electrical engineering or applied physics courses. The emphasis is on the practical design and inherent limitations of the transmission lines, waveguides and antenna systems used in modern communications.

Familiarity with Maxwell's equations is assumed, and the book starts by deriving the plane wave solutions to Maxwell's equations. Boundary conditions are discussed, and reflection, refraction and absorption at interfaces between media are described with considerable mathematical elaboration. Guided waves in transmission lines and wave guides, and waves radiated from antenna, are all introduced as solutions to Maxwell's equations. I have some reservation about whether this approach is the most suitable for all students whose primary aim is to understand the behaviour of practical systems. But the treatment is not very formal, and the authors illustrate their argument with realistic worked examples. The first half of the book is completed with a standard treatment of transmission line theory, discussing reflections and impedance matching, and with a short section on the reflection of pulses.

The second half of the book is devoted to the propagation of communication signals in transmission line, waveguide and microwave systems. Attenuation and noise are considered for all the systems, and the characteristics of cables and waveguides capable of carrying signals over very long distances are described in considerable detail. The generation, reception and processing of signals is not discussed except where it is necessary as part of the explanation of how signals may be changed during propagation; modulation and multiplexing have to be understood, for example, in order to consider the signal degradation due to intermodulation when non-linearities occur in repeater amplifiers. The treatment of propagation is excellent — not difficult, but clearly explaining what is happening in terms of the basic principles given in the earlier part of the book. □

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General geophysics

D.H. Tarling

The Physical Environment. By B.K. Ridley. Pp.236. (Wiley: New York and Chichester, UK, 1979.) £8.50.
Palaeomagnetism and Plate Tectonics. By M.W. McElhinny. Pp.357. (Cambridge University Press: Cambridge and New York, 1979.) £7.50.

RIDLEY'S is an interesting little book designed to provide an awareness of the total underlying physical structure of the environment for students of science and engineering. The scientists to whom the book is addressed include social scientists and it therefore uses a minimum of mathematics in its attempt to provide a unified basis for the comprehension of the relationships between astronomy, geology, meteorology and oceanography. The object is therefore laudible but possibly unattainable within such a small compass unless more rigorous mathematical treatment were introduced. This would then probably lose the innumerate section of his audience, exactly those people most likely to benefit from such a synthesis.

The contents are logically organised, starting in outer space and time, before considering the internal and then external features of the Earth. Halfway through there is a more general discussion of the forces of nature, including nuclear reactions, electromagnetic, chemical and gravitational forces, and then a return to the Earth's surface and the forces operating in and on the oceans. The book then begins a return to the outer limits of the Universe, discussing the Earth's atmosphere, solar and stellar processes and finally considers the origin of the Universe, the Solar System and life.

The tour is thus certainly comprehensive and there is little that can be considered either wrong or over-simplified to the extent of giving misleading impressions. It is thus difficult to pin down a feeling of uneasiness. Some of this almost certainly stems from the style, which is generally very readable but tends to launch into purple prose during either introductory or linking sections. Another reason for unease may be the balance given to different aspects. Four pages on Obler's paradox (and extra reference later on) seems excessively unnecessary when inertial waves are not discussed (only inertial oscillations) yet are virtually assumed within the consideration of wind patterns. Other unease arises from inadequate checking. For example, the age of the base of the Cambrian has different values on different pages. Such errors are trivial in terms of the context, but indicate a lack of care in proof-reading. Another unease is the occasional error — the

magnetic dipole is "inclined" at 11° relative to the Earth's axis of rotation, but this state is to be known as declination.

A final cause for unease is the apparent reliance on the London Geological Museum for many of the geological-geophysical 'facts' and diagrams. While the Museum's exhibition is an excellent one, it is already out of date in some aspects, such as the presence of a basaltic layer beneath the continental granites — a feature that appears in almost all of the diagrams. It is similarly misleading, or indeed incorrect, to say that volcanic activity at subduction zones is due to the melting of light material thrust into the asthenosphere.

In general, the colour diagrams are excellent — mostly derived from the Geological Museum and NASA — but the black-and-white photographs are poorly reproduced, originally colour prints have poor contrast in grey tones, and it seems unnecessary to actually print the *Times* weather map with lettering from the reverse side still showing. The omission of the fold-out weather satellite photographs could have released money for improving other photographs. However, the diagrams are mostly clear and well produced, as is the book as a whole. There are problems at the end (with answers) for those who wish to test themselves; and there is further reading provided for each chapter, although I see no reason that the reading for chapter 5 is incorporated with that for chapter 4 and there is none for chapter 7.

Despite the qualms, it is possible to recommend the book for the general student scientist, although it is clearly designed for a British rather than a world-wide market. One hope is that this may be a short print; a revised edition would be likely to be more strongly recommended.

The second book, McElhinny's *Palaeomagnetism and Plate Tectonics*, is an entirely different proposition. This is aimed at a specific market, the (advanced) undergraduate geologist or geophysicist in particular. When it was originally issued in 1973, this was an excellent introduction to palaeomagnetism and a review of extant palaeomagnetic data. This "first paperback edition" is, in fact, a straight reprint of the hardback edition. Such a term implies to me that some editing or updating has been undertaken and as this is certainly not the case, the publisher's claim that it is "a review of the state of knowledge in the subject", which was justified in 1973, cannot conceivably be justified in 1979. The data base has expanded severalfold since McElhinny submitted the manuscript in, presumably, 1972. There have also been major advances in our understanding of magnetic processes within rocks, the behaviour of magnetic minerals, the instrumentation to measure either the magnetisation or other magnetic properties, and so forth. It is thus invidious to both the author and the reviewer to comment in detail on how certain aspects no longer correspond with current knowledge or awareness. CUP would have been better advised to issue a revised edition. As it is, this book can still be recommended as highly readable and well presented. The production is good and reasonably durable. It is with sorrow and disappointment that one can no longer give this paperback edition the recommendation which the original hardback deserved so well. □

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Solid state physics

W. Cochran

The Solid State. By H.M. Rosenberg. Second edition. Pp.274. (Clarendon Oxford University Press: Oxford, 1979.) Hardback £5.50; paperback £2.25.

THE first edition of this book appeared in 1975 and I feel sure that it was read and enjoyed by most lecturers in solid-state physics, and that they will have recommended it to their students. It is one of the Oxford Physics Series, which the Editor describes as core texts intended to cover material usually treated in the first year of honours courses in English universities, or in the second year in Scotland. The Editor introduces the book as one which succeeds in capturing the

spirit of the stimulating lecture course that Oxford undergraduates have enjoyed for many years from Dr Rosenberg, and goes on to claim that it requires only a fairly basic background in mechanics, electricity and magnetism, and atomic physics, along with relatively intuitive ideas in quantum physics.

The only important difference between the second and first editions is the addition of a fourteenth chapter, on superconductivity. While I liked this chapter as well as any, I fear it will be beyond the scope of students — particularly of materials science and engineering — at the level for which the book is intended. One or two new problems have been added after the earlier chapters, and fourteen after the final one, to give a total of about 120. Numerical answers are now given where appropriate, although the author admits that he views the ensuing correspondence with some trepidation. A new section has

been added at the end of chapter 11, to explain the phenomenon of saturation in NMR and ESR. Otherwise the second edition stays very close to the first. The opportunity has been taken to remove some minor errors: in particular Fig. 8.6 no longer conveys the impression that band overlap occurs at the zone boundary in one dimension. A remaining source of possible confusion is that while page 124 has "we shall use e for the modulus of the electronic charge", in the section preceding a discussion of the Hall effect we read ". . . where e is the electronic charge".

How does Rosenberg's book compare with the dozen or so others which a lecturer might recommend? The author's own list of 'standard texts', with his comments, is as follows:

Solid State Physics. By N.W. Ashcroft and N.D. Mermin. (Holt, Rinehart and Winston:

New York, 1976.) A detailed, higher-level, modern treatment.

Solid State Physics. By J.S. Blakemore. (Saunders: Philadelphia, 1974.) A lively intelligent presentation.

Solid State Physics. By A.J. Dekker. (Macmillan: London, 1960.) A good introductory text.

Introduction to Solid State Physics. By C. Kittel. (Wiley: New York and Chichester, UK, 1976.) A standard text, brim-full with information and data.

Elementary Solid State Physics. By M.A. Omar. (Addison-Wesley: Reading, Massachusetts, 1975.) An introductory text which includes some unusual topics.

Physics of Solids. By C.A. Wert and R.M. Thomson. (McGraw-Hill: New York, 1970.) This is at a lower level than the other texts. It is very well written and illustrated.

Personally I would immediately delete Omar's book from any such list, as it includes a truly astonishing number of errors and misconceptions in its first few chapters, and I would add

Solid State Physics and Its Applications. By R.J. Elliott and A.F. Gibson. (Macmillan: London, 1974.)

Physics students in Edinburgh first meet solid-state physics in an introductory review course of 15 lectures given in the second year. The recommended text book is currently:

Real Solids and Radiation. By A.E. Hughes and D. Pooley. (Wykeham: London, 1975.)

A further thirty or so lectures are spread over the third and fourth years of the honours course. When I gave the third year course I recommended Rosenberg and Kittel, in that order, and in the fourth year I reversed the order. So to give the publishers a publishable quote — A book which we shall certainly continue to recommend to students in Edinburgh. □

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Animal behaviour in laboratory settings

Trevor W. Robbins

The Experimental Analysis of Behaviour. By E. Fantino and C. Logan. Pp.559. (Freeman: Reading, 1979.) £8.40. *Stimulus Control of Behavior*. By H.K. Rodewald. Pp.162. (MTP Press: Lancaster; University Park Press: Baltimore, 1979.) £6.25.

FANTINO and Logan have undertaken the timely but formidable task of writing a student text which attempts to reconcile two often-opposed schools of thought in the study of behaviour: the formulation of general principles from laboratory experiments versus the ethological emphasis upon species-specific behavioural patterns, adaptation to ecological niche and evolution. Generally, they succeed admirably in this well produced and reasonably priced work which takes as its theme the dual ontogenetic and phylogenetic determinants of behaviour.

After a brief historical review of learning theory, basic concepts of operant and Pavlovian conditioning, as well as of "non-associative" learning such as habituation are described. Chapters on stimulus control, conditioned reinforcement, choice and aversive control then follow, but the rather staid headings belie the fascination of the topics subsumed. These include behavioural contrast, attention, concept formation, behavioural chains, self-control, punishment, self-punitive behaviour and "learned helplessness". There are also welcome allusions to the more successful applications of behaviour

therapy such as the "token economy".

From these laboratory concoctions we are delivered quite smoothly across the 'Great Divide' to consider the niceties of courtship in snails and other behaviour in the wild. The ethological section is in many ways symmetric with the previous one, with chapters on species-specific behavioural patterns, "the natural history of learning" and two lengthy surveys of learning in invertebrates. The authors manage to cover taste aversion, specific hungers, imprinting, pigeon-homing, song-learning and the controversies surrounding the famous bee-dance. Considering such breadth, inevitably there are neglected areas. Thus, there is little on motivation, where one might perhaps have expected something on feedback control theory. Similarly, memory and claims of language-learning in animals are barely mentioned. I should have preferred rather less on learning in Protozoa to Platyhelminthes, where so much of the evidence is indecisive. On the other hand, important advances in the neurophysiology and analysis of learning in *Aplysia* are well represented.

The book is best suited for advanced students, as few punches are pulled when discussing theoretical issues. For example, the ramifications of Herrnstein's Matching Law are given an extensive quantitative treatment (though Rescorla-Wagner Theory is conveyed with not one equation!). The authors' boldness in incorporating the most recent material into their argument is also impressive, although the drive to synthesis sometimes obscures dissemination. For example, the critique of the use of 'anxiety' as an intervening variable to explain conditioned suppression seems mis-directed when couched physiologically. Neither was I convinced that satiety is "most likely" not a learning phenomenon (page 42), nor by the somewhat glib explanations of

"vicious-circle" behaviour.

Minor blemishes are the typographical error which makes nonsense of Equation 7 page 241, and frustrating references to unpublished talks at meetings, sometimes by one of the authors (for example, page 283)!

However, the book is at its best in the concluding integrative section when the obvious merits of applying 'laboratory' techniques to ethological problems are made clear with examples taken from optimal foraging and displacement or adjunctive behaviour. Finally, the authors examine the "challenge to reinforcement theory". The challenge, with this book, seems well met.

Rodewald's book *Stimulus Control of Behavior* provides a striking contrast. Here is an unambitious tome which really does justify its perhaps puzzling description as a textbook for undergraduates or a "reference handbook for professionals who will find here a source of useful technology for the study of animal behaviour in laboratory settings". The subject-matter is probably of limited appeal, but is developed in easy steps in the classical pedagogical manner. The book is perhaps most suitable for advanced tuition in practical classes of operant conditioning involving experiments in psychophysics, attention, discrimination or memory. In his book, Rodewald cites some 159 references whereas the corresponding chapter of Fantino and Logan uses 133. It is perhaps of interest that these totals share only 14 references in common. Does compromise between schools of behaviour jeopardise concordance within them? □

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Developmental psychology

James Russell

Human Development. By T.G.R. Bower. Pp.473. (Freeman: San Francisco and Reading, 1979.) \$15; £8.40. *The Functions of Language and Cognition.* Edited by G.J. Whitehurst and B.J. Zimmerman. Pp.313. (Academic: New York and London, 1979.) \$21; £13.65.

THE impression gained from reading these books in succession is that the aim of the Bower book is to review in order to teach and that of the Whitehurst and Zimmerman volume to review in order to present the case for modern functionalism. This is not to imply that Bower's book lacks a consistent theoretical standpoint; rather that the differentiation model which he espouses here, as in his other books, is such a broad one that there is much scope for eclecticism. Thinkers as different as Leibniz, Herbert Spencer, Piaget and, of course, Heinz Werner have presented differentiation models of development, and in Bower's case the framework allows him to support such diverse positions as neo-Piagetianism, social learning theory, and Laingian theory. There is much to agree with in his treatment of the standard developmental topics, but I think that his statement of the differentiation position as implying that concepts develop from the

abstract to the concrete is needlessly paradoxical.

One of Bower's main neo-Piagetian themes is the notion that concepts and skills develop by being replicated on progressively higher levels. Given this, it is difficult to resist the facetious comment that Bower's own writings appear as points on a similar spiral: ideas explored in the early 1970s have now been presented a number of times each with slightly wider degrees of generality and very slightly wider data bases. It is a pleasure to encounter some of Bower's adventurous theorising at his current level (for example, the INRC group being first expressed in infant action) but less than a pleasure to find oneself noting how little of the referenced work has ever or will ever appear in journal form. Bower also evokes the same prissy reflexes by his too brisk treatment of certain topics: the evidence for the genetic basis of schizophrenia, personal construct theory are two such. But in general this book will make an excellent initial text for developmental courses so long as the course leader is at least as healthily sceptical as Bower himself.

Anyone who is at all familiar with the contents of the past three or four years of American developmental journals will feel at home in the Whitehurst and Zimmerman volume. The strength of the book lies in the fact that — as the editors point out — the writers were actively encouraged to make their contributions cohere. They succeed in the attempt, but given that most youngish American developmental psychologists

have already been channelled towards a very definite stylistic and theoretical consensus I doubt if they had to try very hard. This is not meant negatively: the contribution of 'cognitive social learning theory' taken as a whole has been considerable even if the results of individual studies are seldom breathtaking.

Piagetian theory provided the impetus for much of the work reviewed here, but the Pragmatist tradition and experimental methodologies determined its orientation. Most of the contributors repudiate structuralism in cognitive (Piaget), linguistic (Chomsky), moral (Kohlberg) and memory (multistore models) development and most rely on the efficacy of social modelling, concept teaching and verbal rule learning in their arguments. There are many good things to be found: Ornstein provides an excellent comparative review of adult and child experimental work on memory and tries to show where cross fertilisation is and is not possible; Liebert directs a well aimed dart at the Kohlberg bubble; and Rosenthal forges some links between laboratory data and social and clinical problems. Overall this book will prove a useful text for advanced students and researchers who will find the rigorous referencing particularly useful. My only real misgiving is that the 'cognitive' in 'cognitive social learning theory' is being done less than justice here, as elsewhere. Why, after all, do modelling and training work? □

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Personality assessment

Graham F. Wagstaff

Personality. By R. Forgas and B. Shulman. Pp.434. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) £11. *Personal Enquiry and Application.* By M. Sherman. Pp.546. (Pergamon: Oxford and New York, 1979.) £7.95.

I AM sure that anyone involved with the study of personality will find these books valuable reading. Contrary to the approach adopted by a number of recent textbooks in the area, these volumes do not attempt to give an overview of a vast number of theoretical approaches, but attempt to view the subject matter from more specific perspectives. The authors recognise that the area of personality is confusingly diffuse and it is particularly difficult to select material, other than that concerned with descriptions of major theoretical approaches, that does not seem

to give a superficial coverage of virtually all areas of psychology.

In the first two sections of his book Sherman provides a very useful and easily read critical presentation of methodology in the study of psychology, including the basic concepts of experimental design and analysis, correlation research, ethics of research, reliability and validity, and a review of interviewing, questionnaire, projective and behavioural techniques of assessment. In the final section he presents a critical discussion of psychoanalytic and cognitive learning approaches to personality, spending a considerable amount of space on the behaviourism/situationism issue. However, due to this latter emphasis detailed description of individual personality theories is very restricted, and those readers with a more phenomenological bias or who have interests in factor analytic trait theories, may feel that much of the extensive discussion of the principles of behaviourism is unnecessary and gives an unbalanced view of the issues in personality which is not specified in the title of the book.

Ironically, although Forgas and Shulman specify that their approach is a cognitive one, the reader may find that the content is more representative of the general area of personality than that covered by Sherman. The initial discussion seems to be more pertinent to the area of personality and includes guiding postulates for personality theory, and definitions and constructs used in personality theory. This is followed by critical overviews of a variety of personality theories including Freud, Erikson, Murray, Rogers and Lewin. It is not until chapters 5 and 6 that the cognitive orientation is clearly emphasised, and just as Sherman indulges in a description of behaviouristic principles, Forgas and Shulman engage in a discussion of the relationships of the perceptual system to need-related stimuli. In this way they attempt to construe personality within the context of motivation and the way events are perceived. Consequently they reinstate the concept of motivation as a primary concept in the study of personality. This analysis is then applied to personality development, interpersonal behaviour and psychopathology. Although Forgas and

Shulman's analysis is extremely well formulated, the breadth of the subject matter may still leave the reader very unsure as to the boundaries of the area, and for further reading he may decide that he had better read up all areas of psychology.

In spite of the wide content area, the factor analytic approaches to personality are again conspicuously absent. I find the absence of discussion of the theories of Cattell and Eysenck in both books rather puzzling in view of the pertinence of these approaches to issues involving the nomothetic trait and type concepts of personality, the extensive experimental work that has been conducted in relation to them and the ubiquitous presence of

studies using the 16PF and the EPI. I would have thought Eysenck's behaviouristic analysis would have been particularly appropriate to Sherman's discussion of the behaviourism/situationism issue.

Both books assume little previous psychological knowledge of the reader and are easily comprehended. However, I feel that they will be of most value as supplementary, rather than main texts in personality. In this role both are sufficiently individualistic to assume equal prominence. □

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Surveying microbiology

D.G. Smith

Biology of Microorganisms. By T.D. Brock. Third edition. Pp.802. (Prentice-Hall International: Englewood Cliffs, New Jersey and Hemel Hempstead, UK, 1979.) Hardback £17.15. *The Life of Yeasts.* By H.J. Phaff, M.W. Miller and E.M. Mrak. Second edition. Pp.341. (Harvard University Press: Cambridge, Massachusetts and London, 1979.) £10.50.

In these days of multi-authorship of textbooks, it is becoming increasingly rare for a major textbook to have a single author. T.D. Brock's production of three editions of *Biology of Microorganisms* within a decade must therefore be acknowledged as a remarkable achievement and it confers the advantage of a uniformity of style throughout the work.

The third edition follows the general format of earlier editions: the pages are large and attractively laid out although often wasteful of space. The subject coverage remains comprehensive and has been extensively updated to cover recent developments in areas such as recombinant DNA and bioenergetics.

A welcome addition to this edition is the incorporation of what the author calls "vignettes" on historical aspects of microbiology. These occur throughout the text labelled "a bit of history". Although these sections can easily be skipped, an appreciation by students of the historical development of a piece of knowledge is certainly to be encouraged.

Another feature of the new edition is the inclusion of five appendices (42 pages) containing detailed information on energy

calculations, mathematics of growth, biochemical pathways, bacterial classification and microscopy.

This book is one of only two or three available titles which can be recommended as the main textbook purchase by undergraduate students of microbiology.

Now, where would we be without yeasts? For millennia they have been in the service of man making alcoholic beverages and raising bread. They are as domesticated as the cow: no other microorganism is as well known or as widely used.

The second edition of *The Life of Yeasts* is an authoritative but highly readable account of most aspects of the properties and usefulness of the yeasts. The authors set the scene with a brief historical chapter which also introduces us to the fact that yeasts are a heterogeneous collection of fungi from the *Ascomycotina*, *Basidiomycotina* and the *Deuteromycotina*; the unifying features being absence of asexual spores (conidia) and the ability to live as single cells. Six chapters deal mainly with the cell biology of yeasts and three with their ecology and practical applications. Included in the latter is a description of recent developments in the utilisation of yeast cells as food (single cell protein). Yeasts grown on hydrocarbons or carbohydrates are already being fed to animals and there can be little doubt that this will become increasingly important. Another aspect of mounting significance is the spread of pathogenic yeasts freed from bacterial competition by the extensive use of antibiotics.

This book is suitable for the non-specialist at school or college but there is also an appendix containing reference material on classification and characteristics of yeast genera which will be useful to the specialist. □

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Electromagnetic quintet

D.S. Betts

Electromagnetics. By S. Seely and A.D. Poularikas. Pp.790. (Marcel Dekker: New York and Basel, 1979.) £14.40. *Electromagnetic Fields*. By A.M. Portis. Pp.775. (Wiley: Chichester, UK, 1979.) £16.30. *Electromagnetic Fields*. By R.K. Wangsness. Pp.576. (Wiley: Chichester, UK, and New York, 1979.) £10.75; \$20.95. *Electromagnetism: Principles and Applications*. By P. Lorrain and D.R. Corson. Pp.507. (Freeman: Reading, 1979.) Paperback £7.30. *Electricity*. By C.A. Coulson and T.J.M. Boyd. Second Edition. Pp.392. (Longman: Harlow, UK, 1979.) £6.95.

THE first of this quintet is a big book, physically big and big in ambitions, intended for science and engineering students approaching graduation. Seely and Poularikas have set themselves the worthwhile task of developing electromagnetic theory and then applying it within an unusually broad context. This had led to the inclusion of "certain details of acoustics, thermal fields, plasmas, elasticity, physical and geometrical optics". So far so good. The trouble is that these details are rather too often given undue prominence. For example, Chapter 13, "Resonance, Resonators and Coherence", contains four sides of largely mathematical text devoted to the mechanical vibrations of strings and membranes. And in Chapter 8 on wave phenomena the reader finds himself wading through eight sides devoted to longitudinal waves, including a more complete proof of the velocity of sound in gases than is to be found in many basic texts on waves. I feel that in this respect the authors should have exerted a little more self-discipline.

On the other hand there are some very good things. Chapter 7, "Interactions of Charged Particles with Electric and Magnetic Fields", is extremely good, leading naturally into plasmas and the design of fusion reactors. And Chapter 12,

"Elements of Diffraction Theory", gives thorough coverage to a tricky topic; and I also like much of the treatment of waves in unbounded media (not mediums, please!) and guided waves.

The development of the basic equations and ideas of electromagnetism is fairly heavily loaded with references to non-electromagnetic phenomena and this seems to work reasonably well. Three minor quibbles: (1) On pages 236 and 367, it is surely wrong to regard $\nabla \times (\nabla \times \mathbf{X}) = \nabla (\nabla \cdot \mathbf{X}) - \nabla^2 \mathbf{X}$ as a vector identity (except in Cartesian coordinates) — it is a definition of $\nabla^2 \mathbf{X}$. (2) The satisfying proof given that current loops experience dipole-like torques in applied fields does not depend on the loop being plane, so it was a pity to preface the proof by the statement that $\mathbf{m} = I\mathbf{S}$. (3) It is doing Maxwell's equations an injustice to describe (page 363) the charge continuity equation as auxiliary to them — it is built in.

In short, this is a valuable but somehow unwieldy book. It is not helped by its appearance with its typewriter print and spidery diagrams.

In Portis' *Electromagnetic Fields*, again there is a stated aim of putting a considerable amount of applied physical material in with the basic electromagnetic theory. Portis argues that this is more necessary than it was ten years ago because of the decline in the fraction of physics majors (in America) going on to graduate school. It is an argument whose application to the British scene is less than clear. Anyway, the result is a most attractive textbook but one which is fairly expensive and rather too wide-ranging to make large sales in the UK. "The selection of topics has been made within the context of a serious attempt to develop the classical theory of electromagnetic fields from a contemporary point of view." Some of these topics are flagged as being more advanced or specialised (for example, helicons, magnetic dichroism, Aharonov-Bohm effect) and the pages beyond 600 are given over to (valuable) appendices. So the 'core' of the book is in fact of quite manageable proportions, with each of the 15 chapters having a summary and generous number of both exercises and problems. It is well produced with only one noticeable oddity (the text goes down to within a quarter of an inch of the bottom of the page). In reading it, I appreciated the system of numbering topics within each chapter and it was easy to find my way around in. The parts which deal with straightforward electromagnetic theory are organised in a fairly conventional way, with a heavy dependence on vector manipulation in some sections.

Wangsness offers *Electromagnetic Fields* "for use in the usual year-long course in electromagnetism at an intermediate level given for advanced undergraduates". This is a straightforward aim and the text is a good conventional exposition of the subject, with few frills,

up-to-date applications or fancy notions. Putting down Portis and picking up Wangsness one is aware of an enormous difference of attitude and approach. Wangsness gives a comforting feeling of old-fashioned virtue and I hope there is still a market for this. The chapters progress through Coulomb's law, the electric field, Gauss' law (so good to see the apostrophe correctly used), the scalar potential, and so on, in an orderly route which so many of us recognise from lecture courses and other texts. This is not intended as an unkind criticism because I rather like this book with its straight-laced academic air. There is, however, a dilemma: if you write a conventional book on a long-understood topic, in what ways is it better? I think the exercises are a particularly strong point in this case, with 130 actually worked out in the text and another 555 for the student. And the pointing out of common sources of error is helpful. On page 52, for example, the recipe for keeping source points and field points distinguished is good. In short, this is a conventional book, containing very little which could not have been written 50 years ago, but it is done thoroughly and with attention to detail.

It is important not to confuse this book by Lorrain and Corson with another on the same topic by the same authors but entitled *Electromagnetic Fields and Waves* (Freeman, San Francisco, 1970) abbreviated EFW below. The expressed aim is that the present book (*Electromagnetism*, abbreviated EM below) be used at freshman or sophomore (first- or second-year) level "either as an introduction to the subject for physicists and engineers, or as a last course in electromagnetism for students in other disciplines". I presume that those going further would find themselves at home in the other book, EFW, of which I have a good opinion. The present book, EM, I find very satisfactory, with some sense of excitement about it. The examples chosen are often of an applied and modern nature which gives a slight advantage over Wangsness, and there are three chapters on alternating currents which Wangsness leaves out altogether. On the other hand there is only one 22-page chapter on electromagnetic waves, which both Wangsness and Portis are strong on. The general level of production is excellent and the diagrams and problems are admirable, and I can see huge advantages in having a more advanced relation (EFW) to help both authors and readers over sticky patches. In such places, there are footnotes giving references to appropriate points in EFW. The price is, by today's standards, quite modest. It is an attractive book, obviously designed for a large market which I think it deserves to win.

The original version of *Electricity*, by Coulson alone, was published in 1948, and it was used successfully by undergraduates at Oxford and elsewhere for a considerable period. My view of it, as a student, was that

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it was helpful but rather highly condensed and therefore tough-going. Looking at the old edition now, it is clear to me that the difficulty was mainly that I was a physicist and that it was conceived and published as a mathematical text. Thus, there were very few references to experiments or to applications. The new edition has been prepared by T.J.M. Boyd, an applied mathematician, and I find it a very good job, though I would retain the reservation I mention above. There are noticeably more references to physical phenomena and

particularly to plasma behaviour (all the five texts reviewed here give some discussion to plasmas). The units have been converted to SI and some minor improvements of style and coverage have been incorporated. But the main additions are the substantial four chapters at the end, on electromagnetic waves (Chapter 9), waves in bounded media (Chapter 10), the generation of electromagnetic radiation (Chapter 11) and relativistic electrodynamics (Chapter 12). These are good solid chapters which Professor Boyd

has managed to write in such a way that the reader does not experience a style transition on beginning them. The work thus retains a sense of unity. Another improvement is in the use of computer methods for a variety of plotting tasks in which the results and the programs are given. The book is well produced and very reasonably priced. □

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General relativity

D.J. Raine

General Relativity and Cosmology. By J.V. Narlikar. Pp.279. (Macmillan: London, 1979.) £9.95. *General Relativity.* By J. Foster and J.D. Nightingale. Pp.192. (Longman: London and New York, 1979.) Paperback £5.45.

In June 1922, at the height of the deluge liberated by Eddington's confirmation of the bending of light by the Sun, *Nature* reviewed no less than seven books on relativity. In the whole of 1931 it reviewed one. Recent years have witnessed a revival of interest in relativity and a concomitant flux of literature at all levels, especially as part of the centenary celebrations.

Einstein's theory is now half as old as Maxwell's electrodynamics. The fundamental theory has not changed, but much has happened to make the early expositions inadequate. First of all there has been a general diffusion of mathematical ideas, so that extended apologia for departures from Euclidean geometry, or for the mythical difficulties of the theory, are no longer necessary. Secondly, and paradoxically perhaps, with the hindsight of relativity we can now see Newtonian theory in a new way and general relativity can emerge as a necessary consequence of the special theory. Indeed, the teaching of general relativity would be so much easier if only Newtonian gravity were taught, as it so easily could be, in terms of the equivalence principle. But perhaps the most important change, already clear in the established modern texts, is the relentless strengthening of the empirical foundations of the theory which, despite the proclamations, was not finally confirmed by Eddington's expedition. This has culminated in the centenary year in the observations of the binary pulsar, which effectively confirm the existence of gravitational radiation, and play for general relativity a role similar to that of the Hertz experiment for electromagnetism.

Thus general relativity has become as much a part of physics as Maxwellian electrodynamics — except that it is not useful for anything — and might be expected to give rise to a corresponding diversity of textbook treatments.

Professor Narlikar chooses to emphasise the physics of general relativity using only that mathematical dress that is decently necessary for proper calculation — no hint of a dual vector space, no definition of a differentiable manifold because, in the traditional expositions, these are not essential for local computations. Foster and Nightingale opt for a more mathematical approach which brings clarity to the structure of the theory but means that, within their limited space, they cannot go much beyond the classical results. Both assume an acquaintance with special relativity, although Foster and Nightingale give a review of this in an appendix.

Narlikar's book starts with a misprint in a sentence which is wrong anyway: how boring it must have been to write this opening! I was prepared to gird up my prejudices. But, in fact, most of the book is a masterpiece of pedagogic lucidity. Symmetries of spacetimes are dealt with properly in terms of Killing vectors, the theory of orbits in the Schwarzschild solution is developed in terms of effective potentials, Price's theorem in the collapse to a black hole and the four laws of black-hole dynamics all receive a mention. There is even space for derivations of the classical cosmological tests. It is a pity that the Robinson-Carter theorem on the uniqueness of black-hole solutions is missing, and that the results from the binary pulsar presumably came too late for inclusion. And the discussion of the black-hole candidate Cygnus X-1 is unfortunately, to put it politely, slightly confused.

Where I really feel obliged to take issue, however, is with the references to current areas of research activity. It is true that what is intended is only a glimpse and not a survey, and nowhere are they explicitly claimed to be representative. It is true also that most authors avoid the potential embarrassment of Time's sickle compass by leaving out where in doubt. The lecture

format helps here (and here only) in lending an impression of informality. Nevertheless, I feel that Professor Narlikar comes dangerously close to confusing for the reader those matters of personal interest and opinion and the consensus view. The general consensus, right or wrong, is, for example, that quasars are cosmological, that the Hoyle-Narlikar theory is neither in accordance with Mach's principle nor even a putative solution to the problem of the existence of spacetime singularities, that the Steady State Theory is under something rather more substantially earthly than 'a cloud', that the Kaluza-Klein five-dimensional theory is awaiting only the funeral arrangements and that it and indeed f-gravity are less likely to produce a unified field theory than the unmentioned supergravity theories, and that interesting progress is being made in quantum gravity by evaluation of the path integral. The uninformed reader may well be left with a false impression of the main thrust of current thinking, which is a pity in such an otherwise admirable exposition.

The main danger in a mathematical approach to the elements of the theory is that general relativity emerges from the differential geometry as one amongst many possible theories, the geometrisation of gravity appearing as pure artistic creation or conventionalism. The idea that the equivalence principle drives one to this vision gets lost somewhere in the multi-linear mappings. On the other hand, Foster and Nightingale do find space for explicit calculations as well as general results, so that a feeling for the inner working of the theory is communicated. The numerous exercises for the reader help in this, being used here to illustrate the theory rather than to develop it further as in Narlikar's book.

The special aspect of both of these books that distinguishes them from the established modern works such as those of Weinberg and of Misner, Thorne and Wheeler is brevity (a distinction which in relation to the latter is fairly universal). Of course, brevity of exposition does not guarantee greater rapidity of digestion. In fact, Narlikar achieves a masterly conciseness, and Foster and Nightingale

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High-Performance Liquid Chromatography. J. H. Knox *editor*

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concentrate on a proper mathematical development of the classical results.

But for a real example of how to write concisely we have to turn to the appendix of Foster and Nightingale. There we are told that if Newtonian dynamics and not special relativity were true, the two mile Stanford linear accelerator would need to be only one inch long. In a nutshell here is the

essence of the status of special relativity; no technological details, no experimental arrangements, for these can be found elsewhere, but a correct overall view in a single picture. Would that it were all so simple. □

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Basic chemistry

C.A. McAuliffe

Introduction to Modern Chemistry. By E. Meyer. Pp.527. (Prentice-Hall: Hemel Hempstead, UK, 1979.) £11.65. *Chemistry: A Conceptual Approach.* By C.E. Mortimer. Pp.815. (Van Nostrand Reinhold: Wokingham, UK, 1979.) £7.50. *Basic Chemistry.* By G.H. Miller and F.B. Augustine. Pp.420. (Harper and Row: London and New York, 1979.) £6.45. *Chemistry for the Consumer.* By W.R. Stine. Pp.496. (Allyn and Bacon: Boston, London, Sydney and Toronto, 1979.) £13.55. *Fundamentals of Chemistry.* By F.H. Redmore. Pp.711. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) £12.30.

I RECENTLY heard it said that one reason graduates from American and Japanese universities are more adaptable when entering industry than are UK graduates is that they benefit from a relatively non-specialised, more inter-disciplinary course than that which UK students enjoy. I think that there may be something in that notion. Certainly, I am, after seventeen years of fairly intimate contact, still amazed at the job which US universities do for the disparate student-entry they receive. The books reviewed here demonstrate quite well, in what they set out to do, just what a varied body they are aimed at. Indeed, it is a mistake for persons not familiar with US colleges not to realise that there is immense variation in college entries both in terms of preparation and ability of freshmen students. This is directly related to standards in US high schools, where teachers are frequently qualified in education but ill-qualified in the disciplines they teach, and also to the fact that since almost all high school students graduate and are thus, in many States, qualified for entry to State universities, the intellectual abilities span the whole spectrum. In turn, the requirement by many universities for students to pass a basic science course sets a daunting task for would-be authors of basic chemistry texts, but one that can be

professionally and financially very rewarding for those who are successful.

Three of the books discussed here are directed towards students who either have never before had a chemistry course or have had very small exposure to chemistry. The text *Introduction to Modern Chemistry* by E. Meyer has for its first sentence in the Preface: "Teaching a course in basic, modern chemistry is often a unique educational experience for the instructor and students alike." It might well be a rare educational experience for a student to teach a course in basic chemistry, but if one should attempt it this is not the text to refer to other students. I think it is sloppy in Chapter 1, where the word gas is carefully defined a number of times, to also to refer to a gas gauge (meaning gasoline gauge). The introductory chapters seem to be written at an extremely elementary level. Despite my introductory paragraph, I feel it is insulting to any college student to include a half-page illustration of a mediaeval king with a pipe running from his nose to his finger tip to say that early standards of length had some anatomical origin.

There are two and a half pages of photographs of balances (pp. 34-36), and in the worked Example 2-4, one-third of a page is needed to convert 98 mm to 9.8 cm. On page 63 of this college chemistry text it is stated "Each element is associated with a unique symbol . . . In place of carbon, we write C; for chlorine, Cl; for sodium, Na; and so on." Yet, only a little later (pp. 110-125), the Bohr model of the atom and quantum mechanical model are discussed.

It appears to me that authors such as Meyer should ask themselves just who they really are writing for. It is not conceivable to me that one can aim introductory chapters at students who cannot be numerate and are slow to learn, and expect these people to go so quickly from converting °C into °F to a discussion of the emission spectrum of the hydrogen atom. These same criticisms apply to *Basic Chemistry* by G.H. Miller and F.B. Augustine. On page 11, worked Example 2.1 takes two-thirds of the page to calculate how many centimetres there are in 25.00 m. Worked Example 3.3 answers the question "What is the mass of a chromium atom" with the unhelpful: "It is 52/12 the mass of a carbon atom." On page 105 the section on oxidation numbers is inconsistent and

downright misleading. As in many such texts there appears to be poor judgement as regards what it is that is important for a chemistry book to contain; for example only two pages are devoted to the chemical properties of hydrocarbons.

The third of these volumes, *Fundamentals of Chemistry* by F.H. Redmore, is to be recommended. It does contain the trivial chapter (centimetres into inches), but after that it does assume the reader is of at least average intelligence and, in contrast to the Meyer and Miller/Augustine books, it is tightly written, and, like a number of good freshman chemistry texts, is able to simplify quite difficult theoretical concepts. Thus, simple molecular orbital and crystal and ligand field theory are very well presented. The structure of the atom is introduced early (Chapter 4) and is nicely done. I particularly liked Chapter 21: Periodic Variations. Redmore deals with the Born-Haber cycle — the first two books do not.

The fourth edition of *Chemistry. A Conceptual Approach* by C.E. Mortimer is, we are assured in the Preface, "the most student-oriented edition" yet. (Whatever

next? Orienting textbooks towards students!) But it is a good book and deserves to have lasted so long. Chapter 2 on atomic structure is excellent, and I also particularly liked the chapters on kinetics and thermodynamics. The standard of text and diagrams is high almost throughout (but I did find that molecular orbital schemes using circles for s orbitals and squares for p orbitals was intrusive and detracted from the otherwise well produced figures). There are some more serious objections — wave mechanics is dealt with beginning on p. 41, whilst the concept of a mole is not introduced until p. 152; the student who can understand simple wave mechanics surely doesn't need to have explained what the term molecular weight means (also on p. 152). I also feel that standard and non-standard states need clearer definition.

Chemistry for the Consumer by W.R. Stine is aimed at the non-scientist and intends to provide enough chemical knowledge and principles for an understanding of such concepts as nuclear and radiochemistry, agricultural chemistry, food chemistry, medicinal chemistry and pollution problems. It just

does not quite make it. I find it hard to imagine just to whom the book will appeal. If Stine would write such a book for the scientist he might achieve a more worthwhile object. I think this book has a most severe drawback; figures containing rather complicated chemical formulae coupled, albeit, with simplistic text, does not make for an understanding of chemistry by the non-scientist. Furthermore, although Stine says in the Preface that he hopes the reader will "gain a better understanding . . . of such things as energy, food, . . ." only passing reference to nuclear energy is made and the most important energy-capturing chemical system, photosynthesis, is briefly mentioned in the production of carbohydrate — but the non-scientist will probably not realise that photosynthesis converts solar energy into chemical energy. The word energy does not appear in the index. □

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Unifying concept in organic chemistry

R. C. Poller

Organic Stereochemistry. By Henri Kagan. Pp.166. (Edward Arnold: London, 1979.) Paperback £4.95. Translated from *La Stereochimie Organique*. (Presses Universitaires de France, 1975).

ENGLISH LANGUAGE texts of organic chemistry are markedly derivative, so one might expect Professor Kagan's book to contain some fresh insight into a subject where the French contribution has been central. The reader will not be disappointed. Stereochemistry is seen to be a unifying concept in organic chemistry and it is satisfying to see a diverse range of topics from conjugation, through kinetic versus thermodynamic control, to pericyclic reactions discussed from this single standpoint. The treatment is from first principles and as rigorous as could be expected in a work of this size, though only a brief introductory account of the more marginal topics is possible.

All who teach stereochemistry will have been grateful for the moves toward a more logical and consistent terminology which have been evident in recent years. Substitution of the term "chirality" for the anthropomorphic "handedness" is allowing the too vague "dissymmetry" and the often misapplied "asymmetry" to fall

into disuse. The clear division of stereoisomerism into enantiomerism and diastereoisomerism has liberated us from having to tell our students that the optically inactive meso tartaric acid is an optical isomer of the (+)-form. We no longer have certain cyclic compounds uneasily carrying the banners of both optical and geometrical isomerism and the universally applicable RS/EZ system of configurational notation is especially welcome.

We cannot expect that a text originating in a foreign language should simultaneously present novel viewpoints and a sensitivity to the English nomenclature. Kagan and his translators have chosen to use a mix of the old and new terminology. The deliberately literal rendering of the original has, nevertheless, led to some unfortunate semantic choices, for example, where the usual meanings of the terms "racemic compound" and "racemate" have become exchanged. Finally, although this is an inexpensive book, one has the right to expect a higher standard of proof-reading and, more importantly, better diagrams. The latter are small, not always clear, and occasionally confusing.

Despite these caveats this is a valuable book which is commended to all those who have an interest in organic stereochemistry. □

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Inorganic chemistry

H. A. O. Hill

A Theoretical Approach to Inorganic Chemistry. By A. F. Williams. Pp. 316. (Springer: Berlin, Heidelberg and New York, 1979.) DM98; \$53.90.

To my surprise, I greatly enjoyed reading *A Theoretical Approach to Inorganic Chemistry*. Usually when I hear 'theoretical' and 'inorganic' used in conjunction I reach for my revolver. However this admirable book is so full of good sense that all previous prejudices were overcome.

The first chapter contains the essence of quantum mechanics and atomic theory. The only constituent lacking is the relationship between complex eigenfunctions and the angular momentum operator. The concepts culled from quantum theory are then used to describe polyelectronic atoms and ions, laying to rest in passing such a shibboleth as 'the stability of the half-filled shell'.

The key features of molecular orbital theory are succinctly described in Chapter 2 of which a salutary section discusses hybridisation. The application of molecular orbital theory to the interpretation of the structures of

molecules is the subject of Chapter 3 and how best to begin than with a discussion of Walsh diagrams. The section on transition metal compounds is interesting though I was sorry to find the ligand field parameters, Δ and $10Dq$, treated as if they are necessarily synonymous; and even more to find the Jahn-Teller effect introduced on page 82 without a proper statement of the theorem. However, the author makes some interesting comments on organometallic compounds, not least the description of the 'eighteen-electron rule as an example of electron counting rules that work for no especial reason'.

The discussion of electron-deficient compounds (or rather 'compounds for which the theory previously provided was deficient') and cluster compounds is very valuable. It was good to find the same ideas applied to solids, often neglected in popular modern texts. In the chapter on electronic and magnetic properties, the ideas of C. K. Jorgensen find a suitable home; they have long deserved wider exposure. The Jahn-Teller theorem is now discussed more rigorously and as a bonus (?) a brief mention is made of the second-order effect. It is a pity that the author, having kept firmly to SI units in the rest of the book, reverts to c.g.s. units when discussing magnetic properties.

An important chapter contains an account of alternative methods and concepts. Whether the X-method warrants its position at the beginning of the chapter is debatable. The valence bond model and

ionic model are well treated and the section on Valence Shell Electron Pair Repulsion should be essential reading for all undergraduates. It is hard to think of an idea that has gained such wide yet uncritical acceptance. The section on 'thermodynamics and inorganic chemistry' seems a little out of place in this company especially as it is followed by 'Useful Concepts in Inorganic Chemistry'. Some might take issue with that title since it includes a description of 'Hardness and Softness' which even warrants a subsection on 'theoretical aspects'. Still, as the author states, 'as with other concepts in inorganic chemistry, we should know when they lead us astray'. I found the account of 'Mechanism and Reactivity' and 'Descriptive Chemistry' valuable but that on 'Physical and Spectroscopic Methods' less so though even here, the words, though few, are wise. Each chapter has an excellent bibliography.

I have no hesitation in recommending this book to both those who teach and those who study inorganic chemistry. This is especially so for those about to take examinations though by this time it may be too late for the remedial properties of the book to take effect. We should be grateful to the author for sharing his insight with us. □

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Physical principles of photochemistry

G.S. Beddard

Principles of Photochemistry. By J.A. Barltrop and J.D. Coyle. Pp.213. (Wiley: Chichester, UK and New York, 1979.) £4.95.

THERE are now available several photochemistry textbooks; their emphasis is on photochemical reactions but they deal only briefly with basic photophysics. An alternative approach, such as is in large part provided by Barltrop and Coyle's book, *Principles of Photochemistry*, should be welcomed by undergraduates and postgraduates alike. The emphasis of the book is on photophysics rather than photochemistry (consequently the title is inexact, for only in Chapter 6 is photochemistry really discussed).

After a brief introduction in Chapter 1, Chapter 2 describes time-independent excited-state properties. The Born-Oppenheimer approximation, Franck-

Condon factors, spin-orbit coupling, $n\pi^*$, $\pi\pi^*$ and charge transfer transitions are covered. Also included are excited-state geometry changes, acid-base properties and solvent effects. Curiously, though, simple laser theory (which is dealt with too briefly, anyway) is also included in Chapter 2 rather than in Chapter 3, which deals with time-dependent properties, or in Chapter 5, in which techniques for examining reaction mechanisms are explained. Chapter 3 describes excited-state kinetics, fluorescence, phosphorescence, triplet-triplet annihilation and radiationless processes. The last topic is discussed simply but clearly although in a book of this type a more detailed discussion could have been included, especially considering the wealth of information now available. Quenching of excited states by excimer and exciplex formation, electron transfer and electronic energy transfer are treated clearly and concisely in Chapter 4. The kinetics of these quenching mechanisms are also detailed.

Methods of investigating reaction mechanisms, such as trapping intermediates, CIDNP or flash photolysis, occupy half of Chapter 5. No examples of transient flash spectra are given and the most important modern techniques of submicrosecond flash photolysis are only

mentioned in passing. Similarly, measurement of singlet lifetimes is hardly mentioned except for an example in Chapter 3 of the rarely used two-photon fluorescence technique. The best feature of this chapter are the pages analysing quenching kinetics leading to nonlinear Stern-Volmer plots.

In summary, this book contains a great deal of useful and, on the whole, carefully presented information on the photophysical properties of excited states. Photochemical reactions are only briefly (12 pages) studied. The description of the experimental techniques is a little out-of-date and excludes important techniques such as single-photon counting and nanosecond and picosecond flash photolysis. The book is, however, well written and easy to read; the problems at the end of the book are also interesting and require some thought. The restriction of mathematical treatments to the minimum while retaining clarity should encourage less mathematically minded students to use this book. □

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Atomic collisions

H. Kleinpoppen

Atomic and Molecular Collisions. By Harrie Massey. Pp.309. (Taylor and Francis: Basingstoke, UK, 1979.) £12.

AT LAST, one can say, there is an introductory authoritative text book available on atomic and molecular collisions. The author, Sir Harrie Massey, the grand old master and pioneer in the field, has written this introductory book shortly after the completion of the monumental and comprehensive monographs on atomic collisions (edited by him and his colleagues). The introductory book is suitable both for experts and non-experts in the field and particularly for undergraduate students. The book fills a gap and will certainly be welcomed by the scientific community.

The difficulties in preparing an introduction to atomic collisions mainly result from the nature of the subject. While introductory textbooks on solid-state physics or atomic spectroscopy, for example, can be restricted to the selection of stationary physical processes (which are dealt with by stationary quantum mechanical formalism), atomic collisions require dynamical methods and approximations over a wide range of applications. Even for the simplest colliding system such as scattering between electrons and atomic hydrogen no exact theoretical solutions are available. It was not possible to include sophisticated problems of atomic collision theory in an introductory text book. The book does contain a discussion and interpretation of the collision data required to develop basic concepts of quantum mechanics such as particles and waves and their dualism, the uncertainty principle, and the quantum mechanical description of scattering cross sections. Chapters on such topics include elementary descriptions of atomic and molecular structure. Appropriate experimental technology has been explained within the main text. Only a limited selection of topics on atomic collisions could be considered in this type of book. Nevertheless, the author has covered a broad range of the large field of atomic and molecular collisions and he has succeeded in exposing the full scope of the subject. It is obvious that the selection and detailed discussion of these most interesting topics reflect the mastery and long experience of the author as one of the pioneers in the field. The order of the topics of the book follows the traditional scheme, which is mainly guided by selecting projectiles and atomic and molecular targets: elastic and inelastic electron-atom scattering (including resonance effects, capture,

recombination and attachment processes), collisions between neutral atomic and molecular systems, ion-atom collisions, photoionisation of atoms and molecules, and photodetachment of negative atomic and molecular ions. The last chapter deals with atomic collisions in the Earth's atmosphere, the solar corona and interplanetary space. Seven appendices supplement information mainly on experimental technology.

Each chapter, each section and even each line of the book is excellent, and it reveals the great devotion (and love) of Sir Harrie to the field of atomic collisions. The detailed discussions on selected topics (for example, the Ramsauer-Townsend effect, the glory and rainbow structure in atom-atom collisions, or the selected collision

processes in the ionosphere) are of highest pedagogical standard. As an introduction the book represents without any doubt a break-through; it will be a challenge and precedent for future authors. This is the more important as the research field of atomic collisions is still in an explosive state: new exciting results from atomic angular correlations, from spin effects in electron-atom scattering, and from collisions with laser excited atoms will soon require new editions of introductory textbooks. Sir Harrie has paved the way (as he often did in research) for such future tasks. □

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Nuclear physics

J.M. Reid

Elements of Nuclear Physics. By W.E. Burcham. Pp.422. (Longman: Harlow, UK, 1979.) £7.95.

THE accommodation of a rapidly expanding subject is a constant problem in the construction of undergraduate course syllabuses. The problem has been particularly severe in the case of nuclear physics over the past decade. The generally accepted separation of elementary particles (or high energy physics) as a subject in its own right has not produced any long-term amelioration in the face of the constant ferment of new ideas and approaches in both the low and high energy fields. Defined by the author of the volume under review as "the understanding of the nature of matter at a level deeper than that of the electronic structure of atoms, molecules and solids but not so deep as that of the particle structure of the proton and the neutron", nuclear physics must always find a place in some form in any course claiming to span matter from the macro to the micro level. The case for the study of the subject on the grounds of its practical applications has changed dramatically from the time of its emergence from the shadow of restricted work on nuclear based weapons in 1945. It was then, optimistically, to understand the processes about to provide a solution to the world's recognised energy problems. Today the case might be to provide a background understanding of the use of nuclear techniques in order to circumscribe the risks involved in the reluctant application

of these techniques to socially vital problems.

However, Professor Burcham's latest textbook is not concerned with the practical applications of nuclear physics; it sets out to provide a description of the present state of nuclear structure measurements and to demonstrate what can be learned by the application of quantum mechanics to nuclear models. A previous well founded knowledge of atomic physics, relativity and quantum theory and some acquaintance with the rudiments of nuclear physics are required for maximum benefit to be obtained from this book, as the containment of the material within the limits of a single volume is achieved by very compressed treatment of matters assumed covered in earlier courses. Space is thus gained for a thorough treatment of the single particle shell model, the collective model and the unified model. The final three chapters in which the whole field is reviewed from the standpoint of the electromagnetic, the weak and the strong interactions are particularly valuable. A generous supply of numerical problems is included chapter by chapter and the solutions of a selected number of these are given in an appendix.

The final-year undergraduates for whom the book is designed will in no sense find this an easy text. Those among them who have postgraduate research ambitions will find it an excellent base on which their future studies in nuclear or elementary particle physics can be securely built. In fact for several years to come the text should be suitable reading for postgraduate courses in the field. The volume is put together with the neatness and the authority to be expected from an experienced and respected practitioner in this area of research. □

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Applying electrodynamics to astrophysics

M. Rowan-Robinson

Theoretical Physics and Astrophysics. By V.L. Ginzburg. Pp.464. (Pergamon: Oxford, 1979.) Hardback £25; paperback £10.

PROFESSOR ter Haar has performed the arduous task of translating this advanced textbook by a prominent Russian astrophysicist admirably. Impressive though this book is in several respects, however, I feel it needed a good deal more work on it before it was published in a Student Edition.

A more accurate title for the book would have been *A Treatise on Electrodynamics, with some Applications to Astrophysics.*

Most of the book consists of rather academic discourses on the themes of those great books by Landau and Lifschitz. However, Ginzburg does not have quite the same ability to illuminate abstract principles with simple and concrete examples. The absence of any sub-headings within the chapters makes the book hard to read and limits its usefulness as a work of reference. The neglect of the Western literature on the subject in the references cited (over 80% of the references are Russian and about a third are to papers by Ginzburg and coworkers) will not commend the book to other workers in the field, despite Ginzburg's plea in the Preface to the English edition that this was not so noticeable in the Russian edition and that the book was based on a lecture course. It is precisely this kind of deficiency in a lecture course that one expects to be made good in a textbook. The publishers have managed entirely to omit the first four pages of Chapter 3.

The most interesting and useful chapters for the general astrophysicist will probably

be Chapter 5 on synchrotron radiation and Chapters 15–17 on cosmic-ray, X-ray and gamma-ray astronomy, though the review of the observational situation in these latter areas is rather out of date (the Russian edition appeared in 1974). Not all the formulae given are of sufficient accuracy for contemporary astrophysical applications. In the formulae for bremsstrahlung, for example, the Gaunt factor is assumed to be unity: some space could surely have been found for a discussion of the exact value.

The book remains, however, an important one by a major physicist. The specialist in electrodynamics will find it a useful review of Russian work in the field and the theorist in high-energy astrophysics will find some parts of the book valuable. □

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Introducing meteorology

J.S.A. Green

Fundamentals of Meteorology. By L.J. Battan. Pp.321. (Prentice-Hall: Hemel Hempstead, UK, 1979.) £10.90. *The Atmosphere.* By Lutgen and Tarbuck. Pp.413. (Prentice-Hall: Hemel Hempstead, UK, 1979.) £10.90.

MOST of us have a vested interest in meteorology, and any books like those reviewed here, that seek to explain the intricate details of the subject to a wider audience, are always welcome. These two books summarise modern meteorology for the 'non-mathematician', by which the authors mean one not familiar with 'differential calculus'. Both books cover many topics of interest to a general reader, such as air pollution (supersonic airliners come in for substantial unquantitative criticism), clouds, the generation of rain, storms and climate. Curiously, their contents overlap by some 75%. To a scientist used to a uniform system of units, they both show a wide variety. One has a useful table of densities of common substances expressed in g cm^{-3} , as well as in kg m^{-3} . That the figures in one column are just 1,000 times the figures in the other might well strike the uninitiated as an odd thing for scientists to pay attention to. A variety of basic units is used: calories, watts, feet, metres, knots, metres per second. Presumably the aim is to use units familiar to the reader, but one loses

something of scientific nicety. The literary style is inexorable rather than objectionable: "... precipitation data for localities in selected precipitation regimes ..." is typical.

My only major reservation concerns the sort of information that the authors have tried to present. A typical, but not unimportant, topic concerns the geostrophic wind. This blows along the lines of equal pressure, not across them from high to low pressure, as one might naively suppose. If I had to start from my first sight of Newton's laws of motion in order to arrive at this result, then I think I would feel cheated. The important fact is that the Coriolis acceleration is at right-angles to, and proportional to, the wind and not as one would expect, along the direction of the change in velocity as we usually measure it relative to the Earth. The point is made by having an experimenter, who used to be a golfer (but who now uses intercontinental ballistic missiles), fire missiles from the North Pole while the rest of the Earth moves past relative to the missile. But this rightly leaves me unimpressed because the golfer is in a situation where the real acceleration of the missile is zero, and the apparent acceleration seen from the Earth is fictitious. For geostrophic motion where the Coriolis acceleration balances the force due to the pressure field, it is exactly the other way round: the relative acceleration is small but the real (Coriolis) acceleration is large. Thus, trying to represent what really happens in terms that are too simple, may mislead that thoughtful non-mathematician. It might be better to tell him that geostrophic balance happens and that it is because of the rotation of the

Earth. However, if you go and study mathematics, you can find the inevitable connection between the Newtonian laws and the geostrophic wind.

One expects to find authors representing such differences in philosophy that this topic highlights, and the books do summarise much modern meteorology, with particular emphasis on conditions in North America. Certainly one (but not both) would be a useful teaching aid for any non-meteorologist wishing to give a course on meteorology to American undergraduates. They are a useful *Introduction to Meteorology*, with the mathematical bits left out, and nicely illustrated by satellite pictures. To me they seemed to lack something of the enthusiasm of the authors for their subject. One of them recommends Minnaert's book, *Light and Colour in the Open Air*, to those interested in optics. Minnaert starts his book: "A lover of Nature responds to her phenomena as naturally as he breathes and lives." Now that is the sort of attitude I think we can expect to put before this person who has failed to acquire 'differential calculus' amongst his grades, and it does not come over to me from either of these texts.

Let us hope that their readers will absorb the philosophy and enthusiasm of Minnaert, as well as the useful factual information which he will find in these books. □

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Principles of applied geology

John Knill

Principles of Applied Geophysics. By D.S. Parasnis. Pp. 275. (Chapman and Hall: London, UK, 1979.) Hardback £8.50; paperback £4.95. *Geology for Civil Engineers.* By A.C. McLean and C.D. Gribble. Pp. 310. (Allen and Unwin: Hemel Hempstead, UK, 1979.) Paperback £5.95.

THESE two books, while illustrating quite different aspects of industrially orientated geology, have also somewhat different status as books. Parasnis' book is the third edition of a well known volume which has been reprinted three times between editions, while McLean and Gribble have written a brand new text.

Geophysics has been for many years the major large-scale exploration tool applied to hydrocarbon search, is also widely used in the mineral and construction industries and is now of increasing significance in ocean and land-based shallow crustal studies based on artificial explosions. This text has an extremely systematic approach, separate chapters dealing with magnetic, gravitational, electrical and seismic methods with additional chapters on induced polarisation, electromagnetic methods, radioactivity techniques and miscellaneous methods including borehole logging. The popularity of this book as a brief but comprehensive survey of the field of technique, processing and interpretation in applied geophysics is well justified. The new edition includes a new chapter on induced polarisation, derivation of formulae has been put into appendices to aid the flow of the text and the units and symbolism have been standardised and clarified. This book will undoubtedly continue to fulfill a need for an inexpensive but comprehensive presentation ideal for the student at undergraduate and postgraduate level.

The textbook by McLean and Gribble is primarily directed at the undergraduate civil engineer and provides a basic introduction to geology, and to those aspects of applied geology relevant to the construction industry. The book has a fresh, attractive appearance and the cover is particularly striking, tending to draw the eye, and possibly the wallet. The authors have thought carefully about the philosophy of the book but, in the event, selected the traditional balance between geology and engineering geology on an equal basis. The early chapters review minerals and rocks, engineering soils, stratigraphy and structural geology. The contents are deliberately selective, focusing on those

terms believed by the authors to be of the greatest importance to the engineer. The book then turns to, and deals with, ground and surface water, site investigation including geophysics, rock classification and materials, excavations, slope stability, dams and reservoirs, and tunnels. The chapters on engineering geology draw upon several case histories which are briefly illustrated. There are many clear diagrams and photographs, and each chapter is supported by references. The authors have clearly made a careful attempt to cover the field but there are gaps, some of which are important. For example, there is no reference to soft ground boring techniques, which is surprising after the detailed consideration given to engineering soils, and foundations

appear to be wholly omitted. The authors have drawn mainly upon their own experiences in developing the book and occasionally the text jars to the expert mind. A little more honing of the text in parts would have helped because, to the reviewer, occasional sections or phrases were inappropriate in relation to either conventional practice or the conclusions drawn. However, there is no doubt that the audience for whom the book has been written will find it easy to read, interesting and possibly stimulating. □

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Chemical ecology

P.E. Howse

Introduction to Chemical Ecology. By M. Barbier. Translated by M. Ferenczi. Pp.128. (Longman: London and New York, 1979.) £3.95.

MICHEL BARBIER, a natural products chemist, attempts in this book to review our current knowledge of toxins, defensive secretions, plant allomones and sterols, and to define chemical ecology as a discipline.

My first criticism concerns Mr Ferenczi's translation, which does a disservice to the author. He frequently fails to find the appropriate English idiom, resulting in absurdly tortuous expression as, for example, in the quotation in the paragraph below. His evident lack of familiarity with entomology leads to the common silkworm (*Bombyx mori*) being described several times as a "butterfly" or as the "mulberry tree Bombyx". Worse still, the gypsy moth is described as "the predatory forest butterfly", and the boll weevil as the "predatory cotton plant beetle". It is unfortunate that the publishers did not, apparently, check the translation for syntax, idioms, or use of common names. There are also many minor errors that should have been picked up in proof.

My second argument is with Barbier's concept of chemical ecology, to which he devotes much of two chapters, a preface and an epilogue. He defines chemical ecology as "the science of chemical relationships between living organisms or between living organisms and the mineral world". This allows him to include pollution problems and aspects of nutrient

cycling in the same ambit with animal secretions, hormones and allelochemicals, and to suggest that the whole can lead to a "new philosophy of man" which predicts "the absolute necessity of changing rapidly man's psychology" (that is, in his approach to environmental problems). He (and Ferenczi) make some rather trite observations in terms that render them almost incomprehensible: "... death is a primary condition of life . . . to develop life is akin to increase in death potentials, including various forms of pollution. In this instance, the contradiction is not thought to be fundamental, but rather to be the mirror image of a progress vector". This kind of writing will discourage and confuse any reader, but I firmly believe that such philosophical flights are unnecessary anyway.

Chemical ecology is surely a search to explain interrelationships between organisms and their environment in chemical terms, rather than in terms of traditional ecological factors like climate, niche, food resources, and so on. Chemical ecology is now at a very exciting stage: we now have a good fund of information on the chemistry of animal secretions used in communication and defence, secondary plant substances, and the like. We know very little about the adaptive function of these, but that information is beginning to accrue and the general principles for which Barbier is casting around will be found in the field in coming years. Ecology in general has been concerned for many years with pollution and its effects on natural equilibria, but the methodologies, concepts and supporting disciplines are distinct from those involved in explaining interrelationships between, say a heliconid butterfly, its food plants and its predators, in terms of chemical factors. □

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Ecology booklets

P. D. Moore

Island Ecology. By M. Gorman. Pp.79. (Chapman and Hall: Andover, UK, 1979.) £1.95. *Vegetation Dynamics*. By J. Miles. Pp.79. (Chapman and Hall: Andover, UK, 1979.) £1.95.

THE days are gone when undergraduate texts adequately embraced broad subjects. The development of a whole range of specialist studies even within a field like ecology has rendered it difficult for any one author to deal effectively with the rapidly growing body of information and ideas. Publishers are facing this problem in one of two main ways; either they are turning to edited textbooks in which each chapter has a different author (for example, *Theoretical Ecology* edited by R.M. May (Blackwell: Oxford, 1978)) or they resort to part-works in which various specialists are responsible for brief booklets which are intended to fit together into a uniform whole. This approach has been most effectively pioneered by Edward Arnold in their Institute of Biology series, which now runs to over a hundred items.

Chapman and Hall are now entering this market by producing an ecological series designed on similar lines and edited by George Dunnet and Charles Gimmingham at Aberdeen. The first two issues in this series are reviewed here.

Vegetation Dynamics by John Miles, of ITE (Institute of Terrestrial Ecology), Banchory, is essentially a study in plant succession and it represents a very thorough and up to date review of this area of ecology. It begins by considering the ways in which ecologists view vegetation, with emphasis upon the divergence in viewpoints since Gleason and Clements. Mechanisms of vegetation change are dealt with fairly briefly, which is an unenviable task since such wide subjects as seed dormancy, competition and allelopathy need to be covered in a single chapter. This is not entirely satisfactory, since the subject warrants a book on its own and much has to be conveyed by examples, and no example can ever fully typify an ecological generalisation. In particular, more space could have been given to a consideration of stability, its definition and conceptual value. As it is, one is left with an uncritical statement of Horn's logical, but somewhat unhelpful, definition relating stability to speed of return to the equilibrium state.

A consideration of cyclic changes concentrates upon the well known A.S. Watt examples, plus regeneration of *Abies* forest. It would have been sensible to develop this idea more fully in its application to the persistence of the climax state. The regeneration mosaic of the

climax, as demonstrated by such workers as Loucks, Forcier and Hope-Jones, provides an interesting comparison with the cyclic phenomena described in such detail by Watt.

There is finally a consideration of the role of grazing animals, another subject in which generalisation is difficult. Perhaps its influence on population dynamics of plant species could have received more emphasis.

One area which is rather neglected in the booklet is the total ecosystem view of succession, but perhaps the title was chosen specifically to avoid this issue. Nevertheless, a more complete work would have resulted if the Odum analysis of succession (which is mentioned) had been critically discussed. Such subjects as energy flow and nutrient cycling are central to an understanding of succession.

Overall, I wish the booklet could have been a little longer to include these additional items. Within the spatial confines of 80 pages, Miles has produced an extraordinarily extensive review of over 300 papers and has collated them in an interesting and thought-provoking manner. I shall certainly direct students towards it.

Island Ecology by Martyn Gorman is concerned with a very much more confined topic than vegetation dynamics and thus is more easily dealt with inside the restricted space available. The subject is again one which is of interest to many ecologists because of the manner in which the

biogeographical principles propounded by McArthur and Wilson have been applied generally to fragmented habitats at a variety of scales.

The bulk of this booklet is concerned with true islands and their biology, but the idea of 'habitat islands' is always held in mind. For example, when considering dispersal, reference is made to B.N.K. Davis' experiments with nettle clumps and their invasion by invertebrates.

The mathematics of island biogeography is dealt with in a clear and simple manner and will provide a useful starting point for introducing students to this concept. The evolutionary significance of islands is also considered. The final two chapters are devoted to habitat fragmentation, both on the scale of mountain ranges and at the nature reserve level.

The bibliography for this topic is, not surprisingly, considerably smaller than that for vegetation dynamics. The editors should have insisted upon a uniformity of arrangement of references which, in this book, are placed at the end of chapters.

This new series has commenced with two useful and readable booklets and subsequent titles must be awaited in hopeful anticipation. Some of the future authors, we gather, will derive from areas other than eastern Scotland; the home team has set them a high standard to maintain. □

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Microbial ecology

P. S. Meadows

Microbial Ecology: A Conceptual Approach. Edited by J.M. Lynch and N.J. Poole. (Blackwell Scientific: Oxford, 1979.) Hardback £19.50; paperback £9.80.

THIS book is a mixture of styles and subjects, and standards — some of them excellent, a few mediocre and one or two very poor. The book is divided into three major sections on (1) the principles of microbial behaviour in ecosystems, (2) microorganisms in their natural environments, and (3) economic microbial ecology.

Much of the first of these is interesting reading, although I am not convinced of the need for a detailed description of the range of microorganisms (chapter 2.1). The mathematical treatment of population and community dynamics in chapter 2.3 is not easy to follow unless one has a good grasp of mathematics. It could have been presented in a simpler way without loss of much detail.

The second section contains the main part of the book with six chapters. Chapters on the terrestrial and aquatic environment are followed by the animal as an environment, extreme environments, aerial dispersal and biological interactions. Parts of these are well presented and interesting; but there are some omissions and a few inadequacies. Much of the chapter on the aquatic environment is to my mind too general, and is not strictly related to microbial ecology except in a very broad sense. For example, the large diagram on the major oceanic gyres is not really necessary. Biological interactions (chapter 3.6) contains two pages on the rumen and caecum (a field that would not be regarded as ecological by some ecological purists), whereas the relationships between microorganisms and invertebrates in sediments and on solid surfaces in aquatic environments receives hardly any comment.

The last major section — on economic microbial ecology — has one first-rate chapter on nitrogen fixation, two chapters of variable standard on microbial spoilage of food and on water pollution, and one quite extraordinary one on recalcitrant molecules.

The book has excellent parts to it.

However, I have three major criticisms. The first stems from the book being a compilation of chapters by different authors. This has led to fragmentation, but not to an unacceptable degree. The second is more serious. Some of the diagrams are impossible to understand except after long contemplation (Figs 3.2.6, 3.2.17, 3.5.8, 3.5.12), which is a pity because some are

models of clarity (Figs 2.2.12, 3.2.15). The third criticism is one about writing English. Parts of the book are badly written and this can only reflect on the authors. The introduction and epilogue and especially the chapter on recalcitrant molecules should not have been published in their present form. They are often long-winded, difficult to understand, and grammatically

wrong.

All of this is a pity because many other parts of the book are very readable and interesting. □

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Microbial physiology and nitrogen fixation

C.F. Thurston

Bacterial Metabolism. By G. Gottschalk. Pp.281. (Springer: New York, Heidelberg and Berlin, 1979.) \$23.00. *The Biology of Nitrogen-fixing Organisms.* By J.I. Sprent. Pp.196. (McGraw-Hill: Maidenhead, UK, 1979.) £5.50. *Microbial Physiology.* By A.G. Moat. Pp.600. (Wiley: New York and Chichester, UK, 1979.) £16.95.

THESE books provide an intriguing study of the different approaches that can be taken when writing for students. All three are concerned more or less with metabolic processes of microorganisms, but there is little else in which they are similar.

Bacterial Metabolism, by G. Gottschalk, is accurately described by its title. It is about the biochemical transformations achieved by prokaryotic organisms and in my opinion is the best concise treatment of the subject available. The text is clear and well illustrated with metabolic schemes and much tabulated information. It starts with a chapter on bacterial nutritional requirements and types which is followed by two large chapters: "How *Escherichia coli* synthesises ATP during aerobic growth on glucose" and "Biosynthesis of *Escherichia coli* cells from glucose". These chapters set a framework which is built on in subsequent chapters to form a very complete picture of bacterial metabolic activity, showing the variations exploited when different substrates for growth are used and/or when different organisms are involved. For instance, the descriptions of catabolic activities of aerobic heterotrophs and of chemolithotrophic modes of metabolism are more thorough and detailed than in any other comparable student text book I have seen. Of the topics included, protein biosynthesis has the least generous coverage; but as this is so well described in many modern textbooks of molecular biology and/or general biochemistry its coverage here is sufficient. All chapters have an informative summary and there is a list of titles for further reading, and subject indexes. The last chapter concerns the fixation of molecular nitrogen, which is dealt with from a biochemical

standpoint, consistent with the rest of the contents of this readable and informative book.

Nitrogen fixation in the broader context is the subject of *The Biology of Nitrogen-fixing Organisms*, by J.I. Sprent. The very wide range of prokaryotes which are able to fix gaseous nitrogen are described with something of their classification. This is integrated with descriptions of the other organisms with which many nitrogen fixers are involved in elaborate symbiotic relationships, although in the case of nitrogen-fixing lichens this treatment is brief. The second chapter examines the biochemistry of nitrogen fixation, including properties of nitrogenase, sources of energy and reductant and some mechanisms which allow nitrogen fixers to reduce or prevent the oxygen inhibition to which nitrogenases are very sensitive. This chapter is not always easy to follow and is illustrated with diagrams which lack clarity, for instance in Figs 2, 3, which show the photosynthetic electron transport chain of *Anabaena*, it is obscure as to where reducing equivalents originate. I was also most disappointed that there was no inclusion of the genetics of nitrogen fixation. The conventional genetic analysis of the *nif* genes of *Klebsiella pneumoniae* and the more recent studies using the techniques of 'genetic engineering' at Sussex and Harvard have contributed much towards the understanding of nitrogen fixation and for many people (whether rightly or wrongly) suggest a possible way for dramatically improving the productivity of world agriculture. I think it was wrong to omit this work altogether.

The following three chapters discuss nitrogen fixation in relation to agriculture, forestry and natural ecosystems. They are an absorbing account of research in plant physiology and experimental ecology presenting much original data showing the importance of fixation to the nitrogen economy of different ecosystems, and the considerable challenge presented to biologists wanting to understand what limits the quantity of nitrogen fixed in the field and what might increase the amount of fixation. The final chapter describes possible evolutionary relationships of nitrogen-fixing organisms and is followed by an informative appendix describing methods of measuring nitrogen fixation. The text is well supported with references, as many as 100 for some chapters.

Microbial Physiology, by A.G. Moat, also uses specific references throughout the text which are listed at the end of each chapter, but otherwise it has little similarity with Dr Sprent's book. According to its dust cover the book draws together the current knowledge of the fine structure (cell structure, substructure), metabolism, and genetics of microorganisms and describes the interaction of these physiological activities in the growth of microbial cells. . . I find this approach to what constitutes the physiological activities of microorganisms curious and I am confident that others will be equally surprised to find the first 120 pages of a book with this title devoted to classification and cell structure. From Professor Moat's preface it emerges that this is substantially a course book for his students and reflects an interesting and broad ranging course in general microbiology, albeit with a physiological emphasis. It is also directed particularly at "students who will ultimately choose to work outside the immediate realm of microbial physiology". I think other microbiology teachers may find the choice of material and the relative depth of coverage not well suited for their students.

The book is well illustrated and contains a lot of detailed useful information, but classification, cell structure, microbial genetics and morphogenesis together occupy over a third of the text. Consequently, I feel it is unfortunate in a book of this size and price that some truly physiological topics are omitted and others are given relatively scant attention. For instance, growth is the subject of one chapter, but the relationship between limiting-nutrient concentration and growth rate is not described; continuous (chemostat) culture is mentioned only twice, in passing, is not defined and is illustrated by a schematic diagram (Fig. 9-5) where the growth chamber contents would regularly siphon out — it is in fact a recycling fed-batch culture apparatus! Parameters such as growth yield and maintenance energy are not mentioned and macromolecular turnover gets little attention. There are substantial chapters on carbohydrate metabolism and energy production, on nitrogen metabolism and on amino acids, purines and pyrimidines, but I was unable to find a description of any mechanism for nutrient uptake or how such a process may be driven at the expense

of metabolic energy. I think I can accept that a course in microbial physiology does not have to include the *lac* operon of *E. coli* as an example; but I deplore the absence from a textbook of the subject, of any description of the control system of a well studied inducible operon, such as *lac*, *ara*, *gal* or *hut*. I was also surprised to find only occasional mention of catabolite repression, with in one instance, a hint that this might be a cyclic-AMP mediated phenomenon; indeed the unqualified and unsupported statement that "the enzymes of the glyoxylate bypass are repressed . . . by a process known as catabolite repression" infers a broader definition of this phenomenon than I have encountered elsewhere. Another area of confusion concerns the assimilation of carbon dioxide by phototrophic microorganisms. First, the text states "Photoautotrophs . . . fix carbon dioxide via either the reductive pentose phosphate (Calvin-Benson) pathway or the reductive C_4 -dicarboxylic acid (Hatch-Slack) pathway. These systems were first discovered in green plants". I would infer that the unicellular green alga *Chlorella* (with which Calvin's group worked) is regarded by the author as a green plant and not a microorganism, were *Chlorella* not specifically mentioned as a group of organisms included in the eukaryotic protists (page 12). Second, Fig. 3-21 entitled "The reductive C_4 -carboxylic acid (Hatch-Slack) cycle" is actually the reductive (or reverse) tricarboxylic acid cycle proposed by Evans, Buchanan and Arnon, which is dependent on two ferredoxin-catalysed carboxylation reactions characteristic of anaerobic metabolic systems and which are not present in the higher plants which show the C_4 pattern of assimilation investigated by Hatch and Slack. Indeed the role of phosphopyruvate as a product of CO_2 fixation in the reverse TCA cycle contrasts strongly with CO_2 fixation by C_4 plants where phosphopyruvate is generally considered to be the co-substrate for the key carboxylation reaction.

The reader will by now conclude rightly that I would not recommend A.G. Moat's book, and there are several general microbiology texts I would prefer.

Returning briefly to the other two volumes discussed I am pleased to have read them, I shall return to them again and I think they both represent good monetary value. *The Biology of Nitrogen-fixing Organisms* has an engaging scholarly style and I am sure will be widely read by biology students and others. Gottschalk's *Bacterial Metabolism* is excellent and I will be surprised if it is not extremely popular amongst students and teachers of microbiology and biochemistry for a very long time. □

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Microorganisms in their environment

J.P. Armitage

Microorganisms: Form, Function and Environment. Edited by L.E. Hawker and A.H. Linton. Second edition. Pp.391. (Edward Arnold: London, 1979.) Paperback £8.95.

THE second edition of this undergraduate textbook has changed format. It is now a fashionable large size book with large, bold print and diagrams. Its sixteen chapters, with twenty-two authors (all, except one, from the University of Bristol), have been divided into three sections: biochemistry and physiology, form, size and life cycles of microorganisms, and the activities of microorganisms in their environment.

The strength of the first edition lay in the good mix of prokaryotic and eukaryotic microbiology and the emphasis on their behaviour in the environment. To this end

this edition has added an excellent new chapter on symbiotic interactions.

However, the new format has resulted in many fewer words than the first edition and, rather than keeping or expanding the better areas of the first edition, all sections have been reduced. This results in much weaker coverage of many areas, in particular biochemistry.

The editing has also been hit and miss: for example, *Klebsiella pneumoniae* is referred to as *K. aerogenes* in the first section, but by its correct name in the second; *Rhodospirillum* has been misspelt and page references to other parts of the book have been left incomplete.

The difficulty with all multi-author textbooks is keeping the level and theme consistent. Unfortunately, by reducing the size of this book but attempting to retain all the subject matter of the first edition the result is a weaker textbook with little to recommend it over the other general textbooks on the market. □

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Soil properties

Stephen Nortcliff

Geography and Soil Properties. By A.F. Pitty. Pp.287. (Methuen & Co Ltd: Andover, 1979.) Hardback £10; paperback £5.50. *Soil Erosion*. By R.P.C. Morgan. Pp.113. (Longman: Harlow, UK, 1979.) Paperback £3.95.

NOTWITHSTANDING the title of this text, the major shortfall of the first book is a failure to place the wealth of information on soil properties into a geographical context. The opening chapter presents a wide ranging review of soils and geography, both physical and human, together with a brief comment on soils and geographical method. In subsequent chapters little attention is paid to geography; rather, the emphasis is placed on detailed descriptions of numerous soil properties.

Although the detailed information presented together with an extensive bibliography of over 40 pages is evidence of considerable effort in compilation, frequently much of the information is presented without a context; also it is not shown why so much detail is important to the geographer. At times less information coupled with more elaboration and discussion would have produced a more complete and easily readable text more

suitable for undergraduate use.

The second book is one of a series of short texts in applied geography suitable for undergraduates studying in the fields of environmental sciences, geography or geology. In a little over one hundred pages the author has set himself the task of making the reader aware of the importance of soil erosion as a problem throughout the world, the mechanics and processes of soil erosion, the factors which influence soil erosion, soil conservation practices and the scope for modelling soil erosion studies, as well as giving some examples of soil erosion studies.

Remarkably the author achieves this, but only by presenting the reader with just a brief outline of each topic. Any additional information must be added by the reader, and to this end there is a bibliography chiefly of erosion studies. As an undergraduate text this approach may be acceptable, but at times a little elaboration or development of the topic would have greatly improved the text. In the introduction the author stresses that although soil erosion has long been acknowledged as a problem in tropical and semi-arid areas, it is increasingly recognised as a hazard in temperate countries. It is a pity that few of the examples used refer to erosion in these temperate countries. □

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Plant systematics and taxonomy

V.H. Heywood

Plant Classification. By L. Benson. Second edition. Pp.901. (D.C. Heath and Company: Lexington, Massachusetts and Toronto, 1979.)

In the 22 years that have elapsed since the publication of the first edition of this work, plant systematics and taxonomy have experienced major changes, but these are scarcely reflected in this new edition. It is intended as an elementary textbook "to open up the new world of living plants to college students and the educated public". The author refers readers to his *Plant Taxonomy, Methods and Principles*

(Ronald: New York, 1962, 1978) for an advanced treatise covering the application of cytogenetic and experimental investigations to plant taxonomy.

On the other hand, new information and ideas on the origin and relationships of the major groups of vascular plants other than the flowering plants are taken into account in the appropriate sections of this edition. For the flowering plants, four new systems of classification, namely those of Stebbins, Takhtajan, Cronquist and Thorne, are considered (chapter 16), though not fully accepted; and the author has presented a revised version of his own system, the most conspicuous change being the final abandonment of the Amentiferae as a partly natural, partly artificial group. No mention is made of other recent systems such as those of Dahlgren and Soó. The section of the book devoted to the classification of natural floras, primarily

with reference to North America, has also been revised.

Overall, this new edition of Benson's major work retains the merits and faults of the original. It is too long (nearly 900 pages) and diffuse and covers too many diverse topics for a single work. It is an excellent book to dip into, but is scarcely likely to recommend itself to students outside North America as a textbook of systematics, although it contains a large amount of information that would be useful for various courses. The book is well printed and illustrated, but the binding in my review copy has already come adrift. □

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Fungal biology

P.E. Long

Biology of the Fungi: Their Development, Regulation and Associations. By Ian K. Ross. Pp.499. (McGraw-Hill: New York and London, 1979.) £11.20.

PROFESSOR ROSS sets out to provide an introductory undergraduate text emphasising developmental and regulatory aspects and has succeeded by presenting, in a conversational style, a lively, questioning and personal account both of the fungi and of the protistan mycetozoa and their allies traditionally studied by mycologists. Some will find, as the author anticipates, that treatments of particular groups or topics offend their susceptibilities but a reasonable balance and wide coverage have been achieved in the three sections that deal with the salient features and developmental pathways of the organisms under consideration; discuss the regulation of their vegetative and reproductive development; and review their associations. The latter, shortest section includes a welcome chapter on viruses in fungi but is really a rather loose mixture, strictly fungal, additionally ranging from their spore liberation and dispersal through saprobic, mutualistic, parasitic and predatory activities to their impact on human affairs.

My initial enthusiasm became tempered by the impression that the survival strategies of the septate higher fungi and their capacity to produce varied multihypal

structures are not sufficiently described. Furthermore the roles of vacuolation and septal pore occlusion in thallus development are neglected as is much experimental work both on conidiation and the cell cycle in yeasts, while hyphal wall architecture and synthesis receive rather cursory attention. To be fair many of these deficiencies can be rectified by diligent use of the extensive bibliography although this remedy is not available for readers of chapters 15 and 16, as, atypically for this up-to-date textbook, few post-1970 books on parasitism or mutualism are cited. Some more generally useful sources are overlooked too, including Ainsworth and Bisby's *Dictionary of the Fungi* (Sixth edition, Commonwealth Mycological Institute, 1971). The figures, mainly in the first section, are good but many lack any indication of scale and some captions are so terse as to be uninformative. Hopefully the appellation 'death cup' that appears under Figure 6.36 will not become perpetuated.

These expressions of vexation denote my exasperation at points which diminished the appeal of a stimulating and attractive book that provides many ideas and much material for a modern course in mycology. The approach is fresh, the arguments enjoyable and some topics are new in a text which will be particularly useful to students who have had some previous exposure to university level cell biology, while also providing food for thought to their instructors. □

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Introductory soil science

D.L. Rowell

Introduction to the Principles and Practice of Soil Science. By R.E. White. Pp.198. (Blackwell Scientific: Oxford, 1979.) £8.50.

ALTHOUGH there have been several books published recently which deal with soils from a geographical viewpoint, this is the first book of its kind to appear for many years. It is a valuable attempt to present soil science at an introductory level, and has successfully shown how biology, chemistry and physics are integrated in the study of this part of our environment. It is thoroughly up to date, including for the first time at this level much that has been understood only recently.

The first two sections deal with the principles of soil science and the third part looks at the application of these principles to soil management, primarily from an agricultural point of view. The book is suitable for use in a wide range of courses at universities, technical and agricultural colleges. It assumes O level knowledge of the sciences, but occasionally starts at a higher level — surely a mistake for a book of this sort. Material is presented very effectively in diagrammatic form. The text is sometimes very concise, perhaps making it difficult for the book to be used in isolation from taught courses. □

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FOR those of my generation who studied plant physiology during and immediately after the second World War choice of textbooks was extremely limited. Now the situation has changed dramatically and students in the 1980s have a wide range of attractive texts some of the more successful of which have recently appeared in new editions. Comparison of a lavishly illustrated modern textbook such as Bidwell's *Plant Physiology* with those that were available to me in the 1940s shows how much the standards of book production have improved in the intervening years.

A popular successor to James' *An Introduction to Plant Physiology* as an introductory text is Baron's *Organization in Plants*. First published in 1963 the book has been extensively revised for the third edition. Like his predecessor, Baron places great emphasis on the encouragement of practical work and it is good to see graphs summarising data obtained in class experiments illustrating the text. An appendix gives details of a number of experimental procedures which should be well within the scope of most school laboratories, and a useful starting point for student projects. Some advice about the design of experiments and simple statistical procedures for the analysis of results would be a welcome addition to this section. A new chemical nomenclature, which I assume is now being taught in schools, is used throughout the book. I suppose that we shall all get used to it in time, but is it really wise to call acetaldehyde ethanal which can be so easily confused with ethanol, however logical it might seem to be? It is something of a relief to be informed that acetic acid for some unexplained reason is still acceptable to the powers that be.

Nowadays a problem for writers of plant physiology textbooks is the lack of general botanical knowledge among their readers because the teaching of traditional botany in schools has almost ceased. To overcome this, Baron provides some background information about the structure of plant cells, but for vital details of plant anatomy the student must go elsewhere. It is a pity that the list of books for further reading at the end of chapter 1 does not include a textbook of general anatomy.

Bidwell's *Plant Physiology*, the first edition of which appeared in 1974, is one of several excellent textbooks by North American authors which give comprehensive coverage of the whole field of plant physiology at a fairly advanced level. Although like most other contemporary texts it concentrates mainly on the physiology of flowering plants with particular reference to those crop plants which have been studied intensively, there is a section devoted to the physiology of what are described as "special" organisms. These include trees, as one might expect from a Canadian-based author, macroscopic algae, parasites and

symbionts. In keeping with modern trends space is found for such topics as the effects of stress on plant growth and the influence of man on his environment.

Students who wish to learn more about the physiology of trees should turn to Kramer and Kozlowski's *Physiology of Woody Plants*. This book is an amalgamation and up-dating of two earlier books by the same authors. It is written primarily for foresters and arborists but inevitably it contains a good deal of general physiology. Biochemical topics are reviewed rather briefly and the book concentrates on more physiological and ecological aspects of plant physiology. There are useful chapters on the structure of wood and the characteristics of tree

How plants work

James Sutcliffe

Plant Physiology. By R. G. S. Bidwell. Second edition. Pp.726. (Collier-Macmillan: London and Basingstoke; Macmillan: New York, 1979.) £14.25; \$18.95 in USA. *Organization in Plants*. By W. M. M. Baron. Third edition. Pp.264. (Edward Arnold: London; University Park Press: Baltimore, 1979.) Paperback £6.75. *Physiology of Woody Plants*. By P. J. Kramer and T. T. Kozlowski. Pp.811. (Academic: New York and London, 1979.) \$35; £22.75. *Plant Metabolism*. By G. Richter. Pp.475. (Croom Helm: London, 1979.) £11.95. *Plant Metabolism*. By H. D. Kumar and H. N. Singh. Pp.302. (Macmillan: London and Basingstoke, 1979) Paperback £4.95. *The Control of Growth and Differentiation in Plants*. By P. F. Wareing and I. D. J. Phillips. Second edition. Pp.347. (Pergamon: Oxford, 1979.) Hardback £15; paperback £7. *Water Flow in Plants*. By J. A. Milburn. Pp.225. (Longman: London and New York, 1979.) Paperback £6.75.

growth. A final chapter is concerned with the influence of environmental factors and cultural procedures on the productivity of forests and orchard crops. The text is supported by a large amount of experimental data and in addition to a substantial list of general references at the end of each chapter there is a bibliography of some 2,200 titles.

Plant biochemistry has been the subject of several new textbooks recently, among them Gerhard Richter's *Plant Metabolism*. This is an English (Americanised) translation of an apparently successful German textbook, *Stoffwechsel Physiologie der Pflanzen*, which was first published in 1969. Although the text has

been revised for the English edition the more recent references quoted are to papers published in 1973 so that in certain areas of this rapidly advancing field the book is already somewhat out-of-date. More than a third of the volume is taken up by an account of photosynthesis which is well presented with the help of clear informative diagrams. The remainder of the book deals with such topics as respiration, the biosynthesis of cellular components and metabolic regulation in a straightforward and fairly conventional manner. No attempt is made to relate metabolic processes to growth but there is a brief incursion into plant water and ion relations and a section is devoted to the role of anions and cations in metabolism.

Extensive use is made of small print when describing experimental procedures and historical aspects of the subject. This enables the author to get much more information into a book of modest dimensions than would otherwise have been possible. However, this and the liberal use of italics throughout the text give the book a rather outdated look which I do not feel will appeal to American readers for whom it is apparently intended.

At less than half the cost of Richter's book one may obtain Kumar and Singh's *Plant Metabolism* which covers very similar ground at about the same level. The new edition of a book which was first published in India in 1976 has been printed there and does not reach the high standard of book production that we have come to expect from the publishers. Again quite a large part of the text is concerned with photosynthesis and as both authors have worked on unicellular algae it is not surprising that algal research features prominently in their account; but there is an adequate treatment of the various pathways of carbon assimilation in higher plants too. The rest of the book is less than inspired, being in the main a rather pedestrian account of the metabolism of nitrogen and sulphur, nucleic acids, proteins, lipids and secondary plant products. In the preface, the authors urge their readers to consult original papers but they provide very little incentive by failing to capture in their writing much of the excitement of biochemical research. Their rather unselective suggestions for further reading including, for example, several outdated textbooks and reviews, are not particularly helpful.

A large part of plant physiology is concerned with the processes of growth and development and there are several textbooks devoted entirely to this subject. One of the most popular of these in recent years has been Wareing and Phillips' *The Control of Growth and Differentiation in Plants* which was first published in 1970. The book is mainly concerned with the effects of plant growth regulating substances on various facets of plant growth. In the second edition the material has been re-organised and parts of the text

have been revised in the light of developments in the intervening years. A comparison of the two editions indicates that apart from advances in understanding of the role of phytochrome in photomorphogenesis, which now merits a separate chapter, and the control of flowering there have been no outstanding discoveries in this field during the 1970's. It must have been somewhat depressing for the authors to find that so many of their pious hopes of advances expressed in 1970 remain unfulfilled in 1978. I think that in the second edition I would have felt inclined to alter the form of words a little and explain why certain problems have remained surprisingly intractable. The picture is not perhaps quite so black as Wareing and Phillips have made it appear

because they do less than justice to the not-inconsiderable advances that have been made in the intervening years in knowledge of control mechanisms at the enzyme level. Fortunately there are other books which remedy this deficiency.

One of the most difficult subjects to put over to students of plant physiology is water relations. Teaching this subject is not helped by the less than adequate treatment of it in many textbooks. Authors of such books would do well to read Milburn's stimulating book on *Water Flow in Plants* before revising this section of their works. Milburn begins by describing the properties of water and he gives a clear account of the concept of water potential before going on to describe various kinds of apparatus by means of which water

movement can be studied. He then describes the water relations of cells and traces the pathways of movement through the soil-plant-air continuum. There is an interesting chapter on responses to water stress and a description of a new device "the oil bomb" which may prove helpful for studying effects of stress on growth.

There is a useful set of appendices containing lists of symbols, units, physical data etc., and a series of numerical problems which will exercise the minds of some university teachers and tutors as well as their students. □

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Vegetation productivity

Melvin G.R. Cannell

Vegetation Productivity. By G. Jones. Pp.100. (Longman: Harlow, UK, 1979.) Paperback £3.95.

describes the author's work on forest growth in relation to soils, and chapter 7 offers some conclusions.

It is a pity that this book was not co-authored or edited by a plant scientist: vegetation is said to "produce" calories (page 14), transpiration is confused with respiration (page 19), a linear regression is said to follow a curve (page 55), and so on. Many figures and tables are poorly explained and both metric and imperial

units are used. Furthermore, the thesis of the book, that a natural plant community provides a measure of the upper limit of vegetation productivity in a given environment, is, at best, highly contentious. □

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THIS little book is an attempt by a geographer to introduce people without any knowledge of plant science to the subject of vegetation productivity in different environments and the ways in which that productivity can be measured. The book is easy to read and may satisfy geography students, but it adds nothing to the books already available on this subject.

Chapter 1 is a introduction to plant physiology, misleadingly entitled "The measurement of plant growth". None of the concepts of plant community productivity are discussed, and photosynthesis itself gets only a brief mention. Chapters 2 and 3 on vegetation productivity contain useful reviews, but readers wanting accurate, balanced and more comprehensive accounts will need to refer to Cooper's book (*Photosynthesis and Productivity in Different Environments*, International Biological Programme 3, Cambridge University Press, 1975) which is not mentioned. Also, anyone seriously interested in measuring forest or grassland productivities will need the handbooks prepared by Newbould (*Methods for Estimating the Primary Production of Forests*, International Biological Programme, Handbook No. 2, Blackwell: Oxford, 1967) and Milner and Hughes (*Methods for the Measurement of Primary Production of Grassland*, International Biological Programme Handbook No. 6, Blackwell: Oxford, 1968) which form the bases of chapters 4 and 6, respectively. Chapter 5

Plant diseases

I.M. Smith

Epidemiology and Plant Disease Management. By J.C. Zadoks and R.D. Schein. Pp.427. (Oxford University Press: Oxford and New York, 1979.) £13.50. *Atlas and Manual of Plant Pathology.* By E.H. Barnes. Pp.325. (Plenum: New York and London, 1979.) £12.35.

It is a pleasure to welcome Zadoks' and Schein's textbook. Plant disease epidemiology has developed enormously in theory and practice in the last twenty years, and the ideas of management in plant protection are spreading from pests to diseases. No university plant pathology course can now fail to tackle these new developments. This new text, though possibly not quite a primer for students with only basic knowledge, provides an excellent introduction to the subject for advanced students. As the authors suggest, the student can choose to benefit from any of the attractive self-contained chapters. They will at all times find clarity of exposition and an interesting and engaging style.

The work builds from the basic level of single infection cycles (monocyclic processes), through population phenomena (polycyclic processes), to the whole pathosystem and its management. It builds from the basic methods of disease control to their integration, from the familiar to the less familiar. It is realistic and critical, and pleasantly free from mysterious jargon.

The core chapter on the essential concepts of epidemiology and their mathematical background is clearly developed and well illustrated, presenting few problems to the not very mathematical reader. There is an excellent chapter on disease and crop loss assessment. Chapters on "Ecological concepts in plant pathology" and "Matters of scale" bridge the sections, the former providing useful comparisons with general ecological concepts.

The text does not make any attempt to deal with the techniques or apparatus of epidemiology, which are perhaps somewhat beyond its scope. However, practical considerations are well in evidence, especially in the assessment chapter, and a most useful feature is the inclusion of simple argued examples from the literature. Many chapters conclude with a useful set of exercises. In conclusion, this is an excellent reasonably priced textbook which will certainly find very wide use in advanced courses in plant

pathology for years to come.

The *Atlas and Manual of Plant Pathology* is, by comparison, not a work of any outstanding interest. A republication of a 1968 edition, with minor modifications, it treats a series of diseases on a taxonomic basis, giving general information on each (causal organism, symptoms, control), together with black and white photographs at macroscopic, hand-lens and microscopic levels. The descriptions are sometimes supplemented by details of laboratory experiments, which are possibly the most interesting part of the work and have not especially dated

since the first edition. However, epidemiology receives little attention. The numerous photographs are certainly useful for the systematic study of plant diseases. However, with a certain prejudice against prepared slides, the present reviewer regrets the non-inclusion of any instructions on how to examine fresh or cleared material. At the other end of the scale, a modern text should surely show some of the insights given by electron microscopy.

The text is also regrettably out of date, and indeed misleading in many respects. Nomenclature is sometimes outdated and

recent developments bypassed (crown gall). Most unfortunate perhaps is the very old-fashioned section on plant virology. The point is that, in this and many other respects, plant pathologists can be quite proud of the progress made in the last decade. It is a pity, therefore, to republish an old textbook, without taking the trouble to revise it. □

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Plant breeding

Barbara Pickersgill

Principles of Crop Improvement. By N.W. Simmonds. Pp.408. (Longman: Harlow, UK, 1979.) £7.95.

THIS is the first new textbook on plant breeding for about 12 years, but a decade is a short time to a breeder so the subject matter discussed remains basically unaltered. Where this book differs from its predecessors is in its excellent treatment of conservation of genetic resources and the green revolution and, more particularly, in its uncompromisingly practical orientation.

Background information on crop evolution, population genetics, polygenic inheritance and heritability is used to discuss the breeder's very real problems of breeding strategy, selection, scale of operations and profitability in either social or real terms. Academically elegant special cases such as aneuploidy in barley or regulation of recombination in wheat breeding get little mention. Indeed, cytology takes a back seat throughout. Tropical crops provide about as many examples as temperate crops, which should increase this textbook's appeal to those teaching in developing countries.

Professor Simmonds writes clearly and concisely but two stylistic traits detract slightly from the book's readability. One is the intentional use of very long captions to tables or figures. By the time one has assimilated those, one tends to have lost the drift of the textual exposition the table or figure was to illustrate. The other is the use of abbreviations. Sentences such as "Thus, summarising the slightly confusing nomenclature of OPP breeding, we have: PIM (varieties propagable as such) contrasted with SYN (varieties regularly reconstructed from parents), with the former based on either MSL or PRT" may completely baffle students who find even basic genetic

terminology difficult. Unfortunately there is no glossary, nor are abbreviations listed as such in the index.

Numerous thought-provoking examples for the reader to work are embedded in the text or captions and carry the textual argument further. It is therefore advisable to do one's homework thoroughly before assigning class reading in this book.

On price, this text compares favourably with most of its competitors. It seems likely to achieve its author's hope of providing a broad general introduction to plant breeding as an intensely practical art. □

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The natural selection

M.J. Lawrence

Introduction to Evolution. By F.A. Racle. Pp.161. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) £5.80. *The Biological Environment.* Edited by J. Lenihan and W.W. Fletcher. Pp.164. (Blackie: Glasgow and London, 1979.) Hardback £9.95; paperback £4.95. *Evolution.* By C. Patterson. Pp.197. (British Museum (Natural History)/Cornell University Press: London, 1979.) Hardback £5.95; paperback £2.95. *Evolving: The Theory and Process of Organic Evolution.* By F.J. Ayala and J.W. Valentine. Pp.452. (Benjamin/Cummings: Menlo Park, California, 1979.) \$16.95. *An Introduction to Evolutionary Genetics.* By D.T. Parkin. Pp.220. (Edward Arnold: London, 1979.) Paperback £6.50. *Evolution.* Readings from Scientific American. Pp.135. (Freedman: San Francisco and Reading, UK, 1979.) Hardback £7; paperback £3.20. *Ecological Genetics.* By E.B. Ford. Pp.442. (Chapman and Hall: London, 1979.) Paperback £7.50.

THIS is a very mixed batch of books which vary greatly in the breadth and depth of their treatment of evolution and related subjects, in their intended readership and in their length. Some, having been written for the layman, assume no previous

knowledge of the subject, while others require at least a knowledge of elementary genetics and biology and are, therefore, of a more specialised interest.

Racle's book, though one of the shortest, attempts to cover the full range of evolutionary studies. Because it is intended for undergraduate non-science majors in American universities and colleges, it contains chapters on elementary geology, which is treated in an historical fashion, and Mendelian genetics. The chapter on population genetics is the least satisfactory not least because it is not at once made clear that the Hardy-Weinberg equilibrium applies only to a population of randomly mating individuals. Discussion of the sickle-cell polymorphism would also have been better done in this chapter rather than in the preceding one dealing with Mendelian genetics. The rest of the book treats the subject in an orthodox fashion and there are chapters on the evidence for evolution and natural selection, on the origin of life, phylogenetic divergence in the plant and animal kingdom, and two chapters on human evolution, though surprisingly, there is little about molecular evolution. The wide coverage of the subject in this short book, which is written in a pleasantly undemanding style, would make it suitable for use in schools.

Lenihan and Fletcher's book is the ninth volume in a series on *Environment and Man* and is intended for "practitioners and students in science, engineering, medicine, administration and planning". It is a rather odd and uneven book with few illustrations or diagrams. The chapters by Fletcher on "Evolution and the Natural Environment", by Ainsworth Harrison on

"Human Evolution and the Environment", by Lenihan on "Is Man a Machine?" and by Smith on "Microbes and the Environment" are straightforward and well written. Jeffers' chapter on "Conservation of the Biological Environment" is authoritative and full of relevant information, though perhaps a little less easy to read than the others. Forbes Robertson's chapter on "Natural Selection in Man" is far too demanding for the intended readership and is, frankly, rather dull. I also have some doubts about the wisdom of attempting to produce a series of books that is aimed at such a wide, semi-professional readership, though with some guidance, this particular volume could also be used in schools.

Patterson's book is a very well written, lucid and up-to-date account of the subject, which ranges from molecular biology to the philosophy of science. Though a short book, it contains numerous excellent illustrations, one of which, on Batesian mimicry in butterflies, is in high-quality colour. The fate of new mutations in a population is particularly well handled. It is to be regretted, however, that the explanation of the concept of fitness is done in terms of gametic rather than the more usual zygotic genotypes (page 58). Fortunately, this has no unfortunate consequences because thereafter the author very sensibly deals with changes in gene frequency in the population in purely verbal terms. Though the book is intended for the layman, its excellence is such that it would be suitable for use both in the sixth form and in the early years of undergraduate courses in biology in universities.

As one would expect from a pair of experienced authors and researchers in the field, Ayala and Valentine's book is a very broad, competent, well illustrated and up-to-date treatment of evolutionary ideas and studies, which, like Racle's book, has been written with the collegiate layman in mind. However, because of its length, the authors are able to deal with the subject in much greater depth than in any of the preceding books. For this reason, the book would serve as an excellent introduction to the subject for the non-specialist undergraduate biologist also. Any teacher recommending the book for this purpose, however, would be obliged to point out a quite unforgivable error in diagrams on pages 31 and 32 which show that the chromosomes are double structures in the early stages of the first division of meiosis, whereas, of course, they are in fact single until late in the pachytene stage. This is such a serious error that it ought to be corrected by an erratum slip at least before any further copies of the book are sold.

Parkin's book has been written for undergraduate students in the biological sciences and assumes, therefore, some knowledge of Mendelian and cytogenetics. Unfortunately, it is a rather uneven book. The first chapter on evolution by natural selection, which gives a sketch of the

historical background, is nicely written as are some parts of most of the following chapters. In far too many places, however, the point that the author is trying to make is not very clear, which is partly a consequence of his having included too many poorly digested examples. There are also a number of errors. For example, the probability of fixation of a neutral mutant is $1/2N$, not $1/2N_e$ (page 34); East and Mangelsdorf, rather than Emerson, were the first to describe the genetics of self-incompatibility in the system found in *Oenothera organensis* (page 103); and heritability is not the proportion of the genetic variance that is due to additive genetic variance (page 114). In addition, several of the figures are either hard to understand or hard to relate to the text (for example, Figs 6.3, 6.5, 7.6 and 8.7). There are also more than a small number of misprints and typographical errors. It is a great pity that the book is marred by these errors for it would otherwise be a useful addition to the literature on evolutionary genetics at this level.

The nine chapters in the *Scientific American* book, which originally appeared in the September 1978 number of this journal, cover the full range of the subject from chemical evolution and the origin of life (Dickerson) to the evolution of man (Washburn). There is an introduction by Mayr and the remaining chapters are by Ayala on "The Mechanism of Evolution", by Schopf on "The Evolution of the Earliest Cells", by Valentine on "The

Evolution of Multicellular Plants and Animals", by May on "The Evolution of Ecological Systems", by Maynard Smith on "The Evolution of Behaviour" and by Lewontin on "Adaptation". Though the articles have presumably been written with the layman in mind, their authority and the excellence of their illustrations are such that they are, in my view, a better introduction to modern ideas about evolution for the intelligent biology student than any of the preceding volumes.

I have deliberately left the best book of the batch until last, for Professor Ford's book is a classic and is nearer to the original literature on the subject than any of the others. Its inclusion in the list arises solely from the fact that it has now most sensibly been issued in paperback form which should make it more accessible to both undergraduate and graduate students in the biological sciences. Though not everybody will agree with all that Professor Ford says, for the book is very much a personal view, he, together with Dobzhansky (and not only the latter, as Ayala and Valentine would have us suppose), have surely contributed more to our understanding of selection in natural populations than any other two men. □

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Genetic variability

Alan E.H. Emery

Laboratory Manual of Genetics. By A. M. Winchester. Pp.148. (C. Brown; Dubuque, Iowa, 1979.) \$5.95. *Investigating Chromosomes.* By A. F. Dyer. Pp.138. (Edward Arnold: London, 1979.) Paperback £6.75. *Understanding Genetics.* Second edition. By N. V. Rothwell. Pp.682. (Oxford University Press: Oxford, 1979.) £14. *The Elements of Genetics.* By I. H. Herskowitz. Pp.442. (Collier-Macmillan: West Drayton, UK, 1979.) *Human Genetics: A Selection of Insights.* Edited by W. J. Schull and R. Chakraborty. Pp.361. (Dowden, Hutchinson and Ross: Stroudsburg, Pennsylvania, 1979) \$30. *Human Genetics: Problems and Approaches.* By F. Vogel and A. G. Motulsky. Pp.700. (Springer: Berlin, Heidelberg and New York, 1979.) DM98; \$53.90.

A NUMBER of textbooks of genetics have been published this year. But they differ so much in approach and content that it is not possible either to compare them or to present them under any unified theme.

Two essentially practical guides which I found appealing are A. M. Winchester's *Laboratory Manual of Genetics* and A. F. Dyer's *Investigating Chromosomes*. Winchester's book is a truly laboratory manual with practical information on such topics as the making of *Drosophila* culture media and the preparation of root tip mitoses (though not animal mitoses). Much of the book, however, is devoted to answering problems relevant to material given in the text. There are work sheets for answers but no solutions are given. It embraces both plant and animal genetics and there are useful sections on human genetics including the preparation of karyotypes from photomicrographs of stained chromosome spreads. For a first course in general genetics this laboratory manual could be most valuable.

Dyer's book is also very practical but at a more advanced level and is mainly concerned with the cytogenetics of flowering plants. The structure and behaviour of chromosomes are studied using essentially one basic preparative technique which is described in detail. It is well illustrated with simple line drawings and photomicrographs, and details are provided of the chromosome constitution of many flowering species. Each chapter concludes with a list of

references for further reading. This book will be of particular value in departments of botany.

Turning now to student textbooks of general genetics we have N. V. Rothwell's *Understanding Genetics* and I. H. Herskowitz's *The Elements of Genetics*. Both authors have had considerable experience in teaching genetics over the years and this is reflected in the clarity of their respective texts. Rothwell's book is perhaps slightly more advanced. Examples are chosen from a wide variety of organisms from phage to man. The sections on molecular genetics are excellent. It is extremely well illustrated with line drawings and each chapter concludes with up-to-date references and review questions, answers to which, teachers will be relieved to hear, are provided at the end of the book. There is also a very good glossary. How this book will fair in the face of many competitors will only be decided by students and teachers who work through it. Certainly it is a very attractive textbook.

Herskowitz's book is basically a simplified version of his *Principles of Genetics* (Collier-Macmillan: West Drayton, UK; second edition, 1977) which I reviewed in *Nature* two years ago and concluded that this is one of the best

undergraduate textbooks of general genetics currently available. But whereas the *Principles of Genetics* is essentially a complete textbook covering the entire field and suitable for a one-year course, the present text will fulfill the needs of a one-term course. For this purpose I have no reservations at all in recommending it. It is very up-to-date and there is also sufficient material on human genetics for those in health science courses. Each chapter concludes with a summary and questions (for which answers are provided), and references for further reading. There is also a glossary of terms. It deserves to be successful.

Finally, two recently published books on human genetics merit special consideration. The first consists of a selection of 26 classic papers in human genetics with comments by the editors, W. J. Schull and R. Chakraborty. This is Volume 10 in a series of *Benchmark Papers in Genetics*. In his Foreword, the series editor, David Jameson, states that papers have been selected which "demonstrate both the development of knowledge and the atmosphere in which that knowledge was developed. There is no substitute for reading great papers". There is little doubt that students should be encouraged to read the original papers in which major contributions to a subject were made. The papers in the present volume are arranged into three sections. The first section is largely historical and deals with the formal genetics of man with selections from such as Garrod, Bateson, Farabee, Landsteiner, Morton, Edwards and Haldane. The second section is concerned with the relationship between genes and chromosomes and human disease, and the selections here include papers by such as Lejeune, Carr, Pauling, Levine and Penrose. The third section is concerned with the nature and maintenance of genetic variability in man and includes papers by Haldane, E. B. Ford, Hirschfeld, Allison and Harry Harris. The editors contribute a final chapter on some of the social, ethical and legal problems which have been precipitated by recent developments in human genetics.

It is interesting to compare this selection with a similar one edited by S. H. Boyer in 1963 (*Papers on Human Genetics*, Prentice-Hall: Englewood Cliffs, New Jersey). Inevitably, and despite protests by the editors of such volumes, the selection of papers for inclusion will reflect, to a greater or lesser extent, the particular interests of the editor himself. Thus, Boyer's book leans more toward biochemical genetics, and Schull and Chakraborty's book toward population genetics. Interestingly the authors of these two books agree on only four papers: Garrod on alkaptonuria and chemical individuality; Pauling on sickle cell anaemia as a molecular disease; Allison on protection from malaria afforded by sickle cell anaemia; and Lejeune on the

chromosome constitution of mongolism. I would therefore recommend both books to any would-be student, though in both he will find little in the area of clinical genetics, for example seminal papers by Carter, Clarke, Lenz and McKusick. Also I think I would take issue with Schull and Chakraborty's stated intention to "... distinguish between those creative acts with no apparent, immediate antecedents and those, which like the specification of the genetic code, may have been creative from the laboratory viewpoint, but represent the culmination of an intellectual ferment so pervasive as to dominate the activities of numerous laboratories. . . . surely a contribution of the former kind does not lie outside the prospects of any gifted scientist whereas the latter too frequently depends on accoutrements rather than insight". I would contend that in science the former is in fact rare and that almost all developments, including those in human genetics, are the result of selection, reshuffling, combining and synthesising of already existing facts, ideas, faculties, and skills. This is of course elegantly argued by Koestler in his *The Act of Creation*. Nevertheless this is an excellent collection of papers and the editors' comments are informative, interesting and germane. It can be highly recommended.

The second book on human genetics is by F. Vogel and A. G. Motulsky, whose expressed aim has been to produce a book which is "... a fairly thorough and up-to-date treatise on the conceptual basis of the entire field of human genetics and its practical applications". In this they have been completely successful. It is as thorough and precise as Vogel's earlier text (*Lehrbuch der Allgemeinen Humangenetik*, Springer, 1961) but is much more modern in outlook with less on anthropology and mathematical genetics. The current text is comprehensive and covers all aspects of human genetics and, as would be expected of authors as internationally regarded as these two, it is authoritative. It is illustrated by 420 very clear figures, and there are over 1,700 references provided for further reading. There is both an author index as well as an extensive subject index, and there are nine appendices into which are collected some of the more mathematical treatments of individual subjects. Despite its thoroughness, however, clinical aspects of the subject are largely ignored. Nevertheless, this is likely to become the standard postgraduate textbook concerned with the science of human genetics for many years to come. It is an excellent book and can be highly recommended. □

Alan E. H. Emery is Professor of Human Genetics at the University of Edinburgh, UK.

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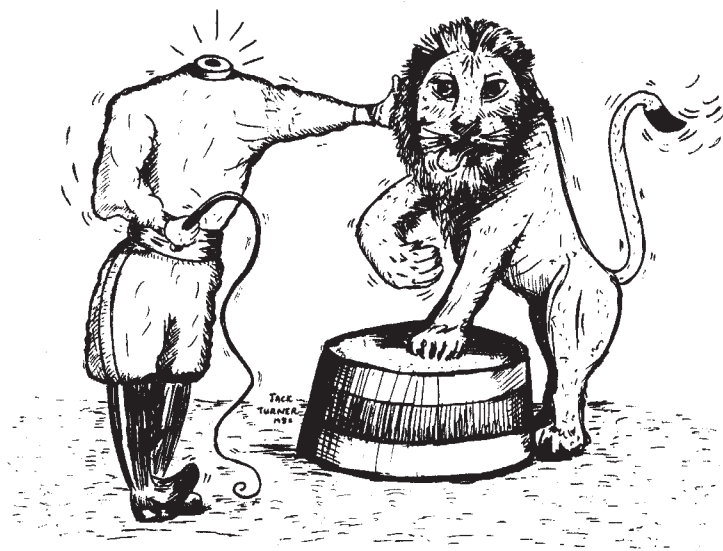
Managing wildlife

T.H. Clutton-Brock

Wildlife Management. By R.H. Giles. Pp.416. (Freeman: San Francisco and Reading, 1979.) £11.40.

As human populations grow and plant and animal populations shrink, it becomes increasingly important for the former to control and manage the latter. The pressing need for trained managers has produced an eruption of wildlife management courses and Giles' book provides an introductory text for this growing market. The book includes chapters on the analysis and manipulation of animal populations, on habitat description and design, on controlling the effects of human populations and on the problems of managing particular groups of animals, from fish to bears.

Wildlife Management is written in an easy, colloquial style, and provides many clearly worked examples of numerical techniques and a list of study questions at the end of each chapter. It has more than its share of facile statements ("Wildlife management is a decision science; an extinct animal is one lacking survivors; all living populations are dynamic"), luxuriant verbiage ("People are an integral part of the population-habitat-people triad of wildlife management (see Figure 1-1)") and unnecessary jargon ("feedforward" for shaping the future of a system; "ecological amplitude" for the range of conditions in which an animal can survive; "opportunity cost" for the compensation that people require to forego behaviour which might harm wildlife). And to an English reader, a proportion of the section headings are ambiguous: for example, it was not immediately clear to me that sections on *Alpha-Person Theory* and *Waterfowl Violations* would deal with analyses of who breaks game laws and the frequency with which legislation involving waterfowl is infringed.



"Don't worry, it'll be all right on the night."

Just what is wildlife is not, according to Giles, very clear. Game species are definitely wildlife but wild flowers, lichens, viruses and nematodes are not. Butterflies may or may not be and fish are sometimes excluded (apparently because of the wiles of a US fisheries commissioner who persuaded Congress to change the name of the US Biological Survey to the US Fish and Wildlife Service, thus providing his particular branch of science with a place in the sun but consigning fish to an ecological purgatory somewhere between birds and invertebrates). This somewhat arbitrary selection, Giles argues, is necessary because "there is a danger of opening a conceptual umbrella so wide that it covers all biology . . .".

But surely this is precisely what wildlife management should aim to do. It is unfair to blame Giles for the implied dichotomy between wildlife biology and ecology since this is common in the wildlife literature. However, the attitude is a dangerous one, especially in an introductory text, for it could cause wildlife managers to believe that they do not require a close acquaintance with ecological and biological theory. This is far from the case and ignorance of

fundamental principles can only produce mistaken management policies. For example, a better knowledge of modern developments in ethological and evolutionary theory would surely have led Giles to modify his views that disease may have evolved as a density-regulating mechanism in some species and can be 'healthy' for such populations; that there is very little evidence for the inheritance of behavioural traits; and that inbreeding seldom has deleterious effects (pages 38 and 75). Such misconceptions could well have a dangerous effect on management policies. Moreover, only a broad understanding of ecological theory will allow managers to predict how previously unmanaged populations are likely to react to novel policies. Wildlife management is not an art form evolving into a separate science, as Giles suggests in his opening chapter. It is one branch of ecology and will only suffer if it is separated from other areas of biology. □

T.H. Clutton-Brock is at the King's College Research Centre, Cambridge, UK.

Adaptation and regulation

D. L. Ingram

Principles of Animal Physiology. By J. A. Wilson. Second edition. Pp.891. (Collier-Macmillan: West Drayton, UK, 1979.) £16.45; \$30.20. *Animal Physiology. Adaptation and Environment.* By K. Schmidt-Nielsen. Pp.560. Second edition. (Cambridge University Press: Cambridge and New York, 1979.) Hardback £22.50; paperback £6.95. *Adaptation to Thermal Environment.* By L. E. Mount. Pp.333. (Edward Arnold: London, 1979.) Hardback £16; paperback £7.50.

THESE three books all share the common themes of adaptation and regulation; but the scope of each is quite different.

Principles of Animal Physiology is a comprehensive textbook covering the whole field of animal physiology, both vertebrate and invertebrate, in nearly 900 pages. It is written entirely by one author and the fact that it is in its second edition must mean that it has been well received. The central theme with which the author has attempted to weld this wide variety of topics together is regulation, an idea which

is in accord with the modern view of physiological systems seen in terms of engineering and mathematical models. A book by a single author has the advantage of the same style throughout; but the subject covered here is so great that it would be very surprising indeed if all the facets were covered with a great depth of understanding.

Just as writing on such a wide range of subjects has its difficulties so does reviewing this type of book, and those chapters which are close to my own subject

inevitably attracted the greatest attention. There are places in the sections on energy exchange and thermoregulation where I feel that the specialised knowledge which can only be acquired by close contact with the subject is lacking and there are occasional errors. The student who comes new to the subject, however, is presented with material which is free from numerous qualifying statements and will learn the more subtle points at a later stage in his study.

The book begins with a section on the properties of living systems in which organisation at the cellular level is covered. In the second section the regulatory systems such as the contractility of cells, the nervous system and hormones are described. Finally, there is a section in which nutrition, thermoregulation, circulation, and water and solute regulation receive attention. There is also a good bibliography. Each chapter is very well illustrated with diagrams and figures, some of which have been taken from published work and some of which are the author's own. Numerous tables provide the student with a wealth of information and there are several charts presenting biochemical pathways and structural formulae of physiologically active compounds. The book is directed chiefly at the American market and would certainly provide enough material for a general degree in physiological zoology. The hard-pressed student will find all the topics covered in his course in a single book and this will have obvious attractions: but the more advanced student will need to consult other texts. The author has not attempted to cover mammalian physiology in the detail which would be required in courses for a medical or veterinary degree for which there are already a good selection of books.

Animal Physiology: Adaptation and Environment, also in its second edition, is a really excellent book, covering as its title suggests a particular aspect of physiology. The author himself describes the book as elementary, and although it is true that the background required is minimal, it would be a mistake to regard this as just an elementary text. There will be very few experienced physiologists who will not gain a greater understanding of their subject from this account. Many topics which may seem difficult in other books are presented here in such an easy manner that the reader has understood the point before he realises there could be any problem. The wide range of research and discussion in which the author has engaged in various places all over the world has provided him with an understanding that ensures that just the right examples are always used to illustrate a point.

The book does not, however, make any claim to being a complete textbook of animal physiology, and although both invertebrates and vertebrates receive attention, the subject matter is

intentionally selective. Physiological systems are dealt with in five parts. The first is headed oxygen and deals with respiration in water and air, and the transport of gases in the body. The second is concerned with food and energy. The third and fourth parts cover temperature, and osmotic regulation. In the final part there is a discussion of movement, integration and the way animals deal with information. The text is well illustrated and there is a good selection of references. I think that this book will serve two functions, one as an introduction which will raise the student's interest, and the other as an account for advanced students who want to organise the mass of facts which they have acquired into an understanding of principles.

Adaptation to Thermal Environment: Man and his Productive Animals is in many respects like an expanded second edition of the author's earlier successful book which was concerned with the climatic physiology of the pig, and is now out of print. This book is much more specialised than the other two reviewed here, being devoted entirely to the thermal aspects of the environment. This general topic has been the subject of several specialised meetings and as in many other branches of physiology considerable progress has been made during the past three decades. The author gives a well presented and highly factual account of the field with particular emphasis on the quantitative aspects of the

subject and includes over 500 references to reviews and original papers.

In the first half of the book the nature of heat exchange between the animal and its environment receives very competent treatment and the physical aspects are presented in a way that should be understandable to students without a detailed knowledge of physics or mathematics. Many of the tables and figures are of use not only as illustrations of the text, but also as a valuable source of reference. In the second half the author deals with the various sorts of environment which animals encounter and concentrates in particular on the reactions of those species which are of economic importance, as well as to man himself.

Students of applied biology will find this book of special value because a great deal of information has been collected from a wide range of sources and presented in a digested form. Although the subject matter is specialised, the book is not an advanced text and is suitable for students with an elementary knowledge of biology and physics. I feel that its particular success lies in demonstrating the ways in which the reactions of animals to their environment are governed by the rules of physics. For this reason it may well find a readership outside the usual scope of biology amongst engineers and designers. □

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All you need to know about proteins

C.C.F. Blake

Principles of Protein Structure. By G. E. Schulz and R. H. Schirmer. Pp. 314. (Springer: New York, Berlin and Heidelberg, 1979.) £13.95.

It is an extraordinary fact, often taken for granted, that just one class of molecule, the proteins, is responsible for *all* the active functional aspects of biological organisms, and for much of their structure as well. Whether one considers catalysis, metabolite transport and storage, molecular defence, blood-clotting, hormonal control, gene expression and muscle contraction; or bone, tendon, membranes and cytosol: in all these processes proteins are the central, active principle. Luckily this vast diversity of protein function is not paralleled by an equivalent diversity of protein structure: in fact the principles of protein

structure are remarkably simple. The past 20 years have seen an absolute avalanche of detailed information on the structure of proteins which now provides a firm foundation for understanding the systematics of protein structure and function.

Schulz and Schirmer's *Principles of Protein Structure* is the first comprehensive attempt to assemble the knowledge gathered over these last two decades. The first part of the book is broadly analytic. Starting with the types of amino acids and the structural implications of the peptide bond, Schulz and Schirmer take us through the covalent and non-covalent forces that determine the patterns of folding and association of polypeptide chains. There then follow chapters on the prediction of secondary structure; thermodynamics and kinetics of chain folding; protein-ligand interactions; and a final chapter on the structural basis of protein function. This second part is broadly synthetic, attempting to use the information from the first part to understand the folding of proteins and the acquisition of function. Unfortunately this logical scheme is interrupted by two oddly positioned chapters on representation of structure and on protein evolution. That

the authors feel some unease at the organisation of the book is indicated by their injunction to begin at chapter 7! That is scarcely necessary; chapter 1 is a good enough starting point, but new readers should be warned that chapters 7 and 9 are misplaced.

Having disposed of this minor criticism,

I can welcome this book with wholehearted admiration. The topic could so easily have led to a diffuse descriptive text, whereas what is presented is analytical and tightly argued. Each chapter is multiply subdivided which makes for easy reference. Lest anyone be concerned about the command of language of two German

authors, Schulz and Schirmer write in a lucid and, at times, elegant English that is never less than a pleasure to read. All in all a totally recommendable book. □

C. C. F. Blake is Lecturer in Molecular Biophysics at the University of Oxford, UK.

Welcome enzymology

G. Lowe

Enzymatic Reaction Mechanisms. By C. Walsh. Pp.978. (Freeman: San Francisco and Reading, 1979.) £18.30.

Enzymology is a subject which has relevance to and devotees from a wide range of disciplines. In this most welcome addition to a growing number of texts the author's approach is based on the chemistry of the reactions catalysed. In this way he has collated the transformations of metabolites in biological systems into a relatively few types of chemical reaction.

The book is in five main sections. In Section I the chemistry of the reactions to be dealt with in the remainder of the book is considered and general comments made on enzyme specificity and catalysis. Section II is concerned with enzyme catalysed group transfer reactions. Acyl-transfer being the most thoroughly studied is considered first. Unfortunately a highly significant paper concerning the catalytic triad of amino acid residues in the serine proteases appeared too late to influence the discussion in the text, but was incorporated as a footnote. This is a nightmare any author faces who attempts to survey a rapidly developing subject.

For a textbook that is devoted to enzymic reaction mechanisms, it is refreshingly free from those algebraic expressions which make enzyme kinetics look so formidable. There is however a very useful account of the application of kinetic isotope effects and reversible inhibition of enzyme catalysed reactions. Glutamyl- and amino-transfer reactions are the subject of the next chapter and this is appropriately followed by two chapters on phosphoryl transfer which includes discussions on phosphatases, ATPases, phosphodiesterases and kinases. This group of enzymes has, however, been the focus of a good deal of attention in the last few years, and inevitably therefore some highly significant experiments concerning the mechanism of these enzymes do not appear. Nucleotidyl and pyrophosphoryl, and glycosyl transfer reactions form the remaining chapters of this section.

Section III which consists of seven chapters focuses on enzymes and their cofactors which catalyse oxidations and reductions. Enzymes using nicotinamide, flavin and pterin co-enzymes are discussed first and this is followed by metallo-enzymes which utilise copper or iron as the redox component in catalysis. Finally molecular oxygen as an oxidising agent is discussed in which one (mono-oxygenases) or both oxygen atoms (dioxygenases) are used.

Section IV is concerned with enzyme-catalysed eliminations, isomerisations and rearrangements. A general theme is less evident in this section. Eliminations and isomerisation are however usually general acid-general base catalysed reactions, whilst rearrangements, which are fairly rare in enzymology, are often dependent on co-enzyme B₁₂.

Section V covers enzymic reactions that make and break carbon-carbon bonds, so bringing together some of the most bio-synthetically versatile reactions, and which frequently require cofactors, such as thiamine pyrophosphate, biotin and pyridoxal phosphate. In the final chapter of this section the chemical logic of metabolic pathways is discussed.

The author is to be congratulated on producing an exciting and very readable account of the chemistry of enzymatic reaction mechanisms. The presentation is excellent, and the text is remarkably free from trivial error. □

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Scope and applications of enzymology

Keith F. Tipton

The Nature of Enzymology. By R.L. Foster. Pp.383. (Croom Helm: London, 1979.) Hardback £19.95; paperback £9.95.

THIS book was an ambitious undertaking in that the author has attempted to survey the properties and function of enzymes and the medical, analytical and technological applications of enzymology at a level that would be suitable for undergraduates reading biochemistry and related subjects such as medicine, pharmacy, and applied biology. In trying to cover such a wide field it is, perhaps, not surprising that some topics are treated in scant detail; for example, there is no treatment of the kinetic analysis of enzyme reactions involving more than one substrate, the treatments of allosteric and cooperative effects are not sufficiently detailed and lack correlation with structural data; and the treatment of enzyme-linked immunoassays is too brief to explain the approaches adequately. Many of these deficiencies are, however, ameliorated in part by the well

chosen references to original papers and reviews.

The mathematical analysis of enzyme behaviour is the weakest aspect of this book and the section on reversible inhibitors contains some confusing errors. In some places, such as the section on the regulation of enzyme systems, the purpose of the mathematical treatments is not made clear.

The strength of this book lies in its treatment of the more applied aspects of the subject, and the sections on the applications and limitations of enzymological methods in medicine and industry are clearly presented and well illustrated with examples. The use of numerous examples to illustrate the points made throughout the book are most valuable and make it enjoyable to read. Because of its somewhat cursory treatments of some important aspects of enzymology I could not recommend this as a textbook for students reading biochemistry as their main subject. Despite the criticisms mentioned above, however, the book might be used advantageously for courses in which biochemistry was a peripheral subject and it could be recommended to anyone wishing to get an idea of the present scope and applications of enzymology. □

Keith F. Tipton is Professor of Biochemistry at Trinity College, Dublin, Eire.

Biochemistry texts

E.D. Saggerson

Elementary Biochemistry: An Introduction to the Chemistry of Living Cells. By Julian Davies and Barbara Shaffer Littlewood. Pp.346. (Prentice-Hall, Englewood Cliffs: New Jersey and Hemel Hempstead, UK, 1979.) *Biochemistry.* By F.B. Armstrong and T.P. Bennett. Pp.491. (Oxford University Press: Oxford, 1979.) £14.

THE stated objective of Davies and Littlewood is to show "that biochemistry is fun" in a book aimed at students not specialising in biochemistry. Whether it is fun or not, the result is a fine book that would make an adequate textbook for any student whose course does not demand the mastery of one of the larger standard textbooks or who wants firstly to read a simpler account of the general features of the subject.

The book, consisting of 16 chapters, has 346 pages of quite small print. The style is simple and attractive and the figures are clear. The scope of the book is quite wide, opening with a chapter on cell structure and organisation, organic biomolecules and the elemental composition of cells. Three chapters are then devoted to protein structure and properties, determination of protein structure (protein separation, sequence determination, X-ray crystallography) and a simple description of enzyme function. The chapter on enzymes does not make recourse to a single equation but manages to describe the salient features of enzyme action together with sections dealing with the use of enzymes in medical diagnosis, industrial uses of enzymes, and enzyme inhibitors. The latter section is interesting since the actions of a number of poisons are discussed together with the actions of a number of antibiotics as enzyme inhibitors.

The general features of intermediary metabolism are covered in approximately 120 pages including, in the section on lipids, discussion of membranes, lipoproteins and the involvement of lipids in heart disease. Two chapters are devoted to nucleic acid structure, transcription and translation including a small section on the use of recombinant DNA in 'genetic engineering'. Human genetic diseases are also briefly considered in this part of the book. Regulation and control are specifically dealt with in a separate chapter which introduces the concept of the operon using the control of the expression of the *lac* operon as an example, briefly considers

regulation of enzyme activity and contains a section on hormones. This latter section, which considers plant hormones and pheromones as well as mammalian hormones, is probably too brief and superficial to deal adequately with the topic but does contain some useful summary tables of hormone structure, source, effect and symptoms of excess or deficiency. The final two chapters in the book are unusual for an elementary biochemistry text. One deals with viruses (structure, life cycle and possible involvement in cancer), the other with antimicrobial agents. There is also an appendix setting out some important aspects of organic chemistry that are relevant to biochemical reactions.

In conclusion, the authors have done well in producing a very sound book which may well appeal to a wide readership.

Armstrong and Bennett's is a general textbook on the subject containing more material than the book by Davies and Littlewood but considerably less than the established textbooks by Lehninger, McGilvery, Stryer, and so on. 467 pages are contained in 24 chapters but the quantity of text on each page being quite small together with a large number of figures means that the content is less than at first sight. The

contents include the history of biochemistry, protein structure, simple enzyme kinetics, carbohydrate, lipid and nucleic acid structure (one chapter on each), coenzyme function, six chapters on metabolism (including one on the basics of human nutrition), a chapter on hormones, and three chapters covering molecular genetics and protein synthesis.

The text is clearly and concisely presented and the figures are good. However, I found the index rather incomplete and there are some serious omissions in the section on intermediary metabolism. Certain aspects of lipid metabolism in particular are grossly neglected. I could find no sections dealing with fatty acid and sterol biosynthesis or with ketone body metabolism. Glycogen metabolism is barely mentioned except when its regulation is used as an example of hormonal control. Gluconeogenesis also received scant attention with no consideration of its physiological role.

Priced at £14, I do not feel that this book will be competitive on the student market. □

David Saggerson is Lecturer in Biochemistry at University College London, UK.

Food provision and energy resources

K.L. Blaxter

Food Energy and Society. By D. and M. Pimentel. Pp.165. (Edward Arnold: London, 1979.) Paperback £3.95.

THE dependence of food provision for man on sources of energy other than contemporary sunshine has been dealt with in a spate of books and articles published in recent years. The Pimentels' book,

through numerous examples in the text and in tabular form, provides a wider basis of illustration of this dependence than most and in so doing a wider perspective. It is designed for undergraduate teaching and will be useful. Indeed, as much of the information quoted is given in original units, it will provide undergraduates with useful exercises in conversion of units to a common basis.

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Early man solving the problems of food provision

The presentation commences with primitive hunting systems of providing food; progresses through simple types of agricultural systems to deal finally with modern ways in which food eventually reaches the dining table and the support energy costs of the many separate processes involved. Such a descriptive account should lead to ideas about strategies to deal with impending future problems. As have others, the Pimentels point to the necessity of stabilising population to stabilise food demand and to the desirability of replacing

animal products by plant products in the human diet so to avoid the trophic axe associated with secondary production systems. These vegetable food products can certainly not be American canned corn for they show that to produce a can containing 455 g corn with an energy value for man of 1.6 MJ entails the expenditure of 12.6 MJ support energy as fossil fuel to process, package, transport, distribute, store and cook the corn. No doubt they had less sophisticated systems for the distribution of primary agricultural

products in mind. It is a great pity that a book designed for undergraduates terminates on the pessimistic theme: "Although man's scientific expertise will help alleviate some of the world shortages, science cannot solve the problems the world faces today". It would have been better, having pointed out the problem, to have emphasised the challenge that that problem poses. □

Sir Kenneth Blaxter is Director of the Rowett Research Institute, Aberdeen, UK.

Marine biology

A.B. Bowers

Marine Biology. By J. Reseck. Pp.257. (Prentice-Hall International: Englewood Cliffs, New Jersey, and Hemel Hempstead, UK, 1979.) £10.75.

JOHN Reseck's book reflects his ideas on how marine biology should be taught to senior classes in schools and introductory classes in universities. The first part deals with physical and biological processes important to the understanding of life in the sea, the second with environments and ecological niches, and the third with taxonomy and characteristics of marine

animals. He places equal importance on interesting and instructing students. The style is direct with short sentences and clear explanations, though word usage and sentence construction will often irritate grammatical purists. Each chapter begins with definitions of technical terms which might be unfamiliar to the reader, and ends with review questions to check his understanding of the material presented. The book is generously illustrated, with more black-and-white photographs than line diagrams. There is a selected reading list at the end and a good index.

The scope of the book is impressive: topics range from primary production to man's use and misuse of the sea, from polar seas to tropical mangrove swamps, and from protozoa to sea-birds and mammals. Most attention is given to North American environments and fauna; the algae deserve fuller treatment. Unfortunately there are many shortcomings in presentation of the

material that could easily have been corrected before publication. Some figures are misplaced in relation to the text. The labelling of several important diagrams is inadequate or inaccurate. Many of the photographs are inappropriate; some of them would puzzle a specialist because the unusual viewpoint, poor contrast and lack of scale make them difficult to interpret. There are careless errors in the text.

The author states that the book is designed for the student to buy and read through, to be complemented by reference books from the library. I would certainly encourage teachers to buy it, but suggest that they make their own decision about recommending it to students in its present form. A carefully revised edition would be very useful. □

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Oceans of literature

R.I. Tait

Oceanography. By J.J. Bhatt. Pp.322. (Van Nostrand, Reinhold: Wokingham, UK, 1979.) £12.10. *Ocean Science.* By K.S. Stowe. Pp.610. (Wiley: Chichester, UK, and New York, 1979.) £9.50. *Exploration of the Oceans.* By J.G. Weihaupt. Pp.589. (Collier-Macmillan: London, 1979.) £12.75. *Descriptive Physical Oceanography.* By G.L. Pickard. Third edition. Pp.233. (Pergamon: Oxford and New York, 1979.) Hardback \$25, £12.50; paperback \$9.95, £5. *Introduction to Physical Oceanography.* By J.A. Knauss. Pp.338. (Prentice-Hall: Englewood Cliffs, New Jersey and Hemel Hempstead, UK, 1979.) £19.45. *Oceanography: Units 1-16.* The Open University Course Team. (Open University Press: Milton Keynes, 1979.) From £3.25 to £7.50 for each of 7 volumes.

To those involved in the teaching of oceanography at University, the choice of suitable text books poses many problems. For introductory courses the range of books available can be divided into two categories: (1) those which attempt to cover all aspects of oceanography; and (2) those which specialise in only one of the related disciplines. The latter group is primarily intended for students wishing to study a particular branch of oceanography or perhaps those who, while specialising in one oceanographic discipline, require a background in another. As courses at University level are usually devoted to one or two disciplines only, category 2 texts are the prime requirement. Books in group 1, on the other hand, normally fall under the heading of "background reading" only. There is an abundance of such books on the market. They are usually lavishly produced, with photographs and diagrams

of the highest quality; a valuable source of visual aids to the teacher but, because of their somewhat superficial treatment of any particular topic, of limited use to the serious student. They do, however, play an important role in popularising the subject and as such they constitute a valuable part of the oceanographic literature.

The group of books reviewed here is divided between these two categories. *Oceanography* by J.J. Bhatt, *Ocean Science* by K.S. Stowe and *Exploration of the Oceans* by J.G. Weihaupt are all good examples of category 1. *Descriptive Physical Oceanography* by G.L. Pickard and *Introduction to Physical Oceanography* by Knauss fall into category 2. The last volume to be discussed, the Open University course *Oceanography, Units 1-16*, although belonging to the first grouping, has a different format: it is basically a students' work book and as such

is unique.

The three books in category 1, Bhatt, Stowe and Weihaupt, all encompass the broad spectrum of the subject including the history of oceanography, the geophysical origins of the Earth and ocean, the physics, chemistry, geology and biology of the sea as well as related topics such as ocean management. All are up to date in their approach to the subject. Of the three, *Oceanography* by Bhatt is perhaps the most attractively produced. Basic definitions are given in a marginal glossary and each chapter concludes with a summary and suggestions for further reading. Effective use is made throughout of photographs to illustrate modern instrumentation.

One consequence of reviewing several books together is that their relative weaknesses become accentuated. Bhatt suffers in this respect. It is about half the size of the books by Stowe and Weihaupt and as it covers much the same field, depth of treatment must suffer accordingly. There is always a danger that too superficial a discussion of any topic may be misleading. To give one example, a student reading the chapter on ocean circulation in Bhatt will not gain an insight into the true nature of the Coriolis force; nor will he understand geostrophic currents, particularly as the illustrative figure is incorrect. And there are many other examples of sketchy treatment. However, in spite of this fundamental weakness there is much good material in Bhatt. Although not of a sufficiently high standard for a University course it will undoubtedly find a place in the school library.

The other two volumes by Stowe and Weihaupt are very similar in content and presentation. Both are eminently suitable for a general course in oceanography or as background reading for students at a higher level. In Weihaupt each chapter is followed by suggestions for further reading; Stowe gives only a summary and no references whatever! However, he does back each chapter with a list of study questions (over 100 in some cases) which is an excellent idea.

Following an introduction to the history of the subject, both texts give a good account of the geological-geophysical aspects of oceanography. Stowe is particularly good on geophysics: he treats the subject at a somewhat higher level than Weihaupt who on the other hand has added an interesting chapter on the changing level of the sea. Climatic aspects of the oceans are adequately covered in both books, but neither author gives sufficient attention to the heat budget of the ocean. Weihaupt is weaker on the dynamics of ocean currents. The T-S diagram receives insufficient treatment in both texts but waves and tides are adequately covered for the intended audience.

Both books have extensive and informative sections on marine biology. As a non-expert in this subject I found

Weihaupt here perhaps easier to read. Each volume concludes with a stimulating chapter on ocean resources and man's impact on the ocean environment. There is little to choose between these two books. If I had to select one it would probably be Stowe, if only because he achieves overall a slightly higher scientific level than Weihaupt. However, both texts are very good. I would rate them as amongst the best books on general oceanography to appear since *The Oceans: Their Physics, Chemistry, and General Biology*. (Sverdrup *et al.*, Prentice-Hall: Englewood Cliffs, New Jersey, 1942).

Descriptive Physical Oceanography by G.L. Pickard is a well known oceanographic textbook which is now in its third edition. As a specialised text it goes more deeply into a physical description of the world's oceans than any of the books discussed above. Where appropriate, some minor changes have been made between the second and third editions to bring the subject matter up to date, but essentially text and diagrams remain unchanged. An important innovation, however, has been the conversion to SI units and the addition of a useful appendix on the units used in physical oceanography.

There is almost no mathematics in Pickard. The author's aim was to cover all aspects of physical oceanography which could be described in non-mathematical terms, with the intention that a companion volume would follow covering the dynamical side of the subject. This volume has at last appeared: *Introductory Dynamic Oceanography* (S. Pond and G.G. Pickard, Pergamon: Oxford and New York, 1978). Together with Pickard's descriptive oceanography it fills a long felt need for a basic text at undergraduate level, or for graduate students embarking on a career in physical oceanography. Whether description and theory should be divorced as completely as they are in Pickard, and Pond and Pickard, is a debatable point. My personal view is that it is a mistake. Integration of description with analysis can often be helpful in the understanding of the latter. (See Knauss below.)

In comparison with all the other books discussed here, the format of Pickard appears very drab indeed. Apart from the cheap production (intentional, but somewhat improved in the third edition) the most obvious shortcoming is the paucity of illustrations. The reader is often faced with unrelieved pages of text, whereas a few simple diagrams would have provided clearer insight with less tedium. I have little doubt that many students find it a rather dull book. However, in spite of this, I shall continue to recommend it to my students: the subject matter is good and presented at the right level for the descriptive part of an undergraduate course in physical oceanography.

In his *Introduction to Physical Oceanography* J.A. Knauss provides a text intended for "beginning graduate students

and upper division undergraduates". As such it is set at a relatively high level of mathematical rigour compared with the other books. Use is made of vector notation and Cartesian coordinates throughout; some specialised derivations relating to the equations of motion and the wave equations are relegated to an Appendix which seems a good idea as it leaves the text free of excess mathematics. Another good point is the clear listing on the inside of both front and back covers of all symbols used. The Appendix also contains four pages of useful tables relating to the physical properties of sea water.

The book is very well written and the material is logically presented. The numerous illustrations of excellent quality are used skilfully in conjunction with a clear prose style, making even the more difficult concepts readily understandable. A reasonable balance is achieved between description and analysis and one of the features of the book is the use, particularly in the dynamical sections, of examples from the real ocean to illustrate theoretical points made. It is perhaps inevitable that not all sections of the book should achieve the same standard. Chapters which stand out as attaining a high level are those on the physical properties of sea water (with the appended tables), the heat budget of the ocean and the four chapters on ocean dynamics, although here some readers may be disturbed by the rather unorthodox development of the balance of forces "without Coriolis" followed by the balance "with Coriolis" instead of the usual treatment of forces "without friction" and "with friction". I cannot avoid mention of one unfortunate error: in Fig. 7.1 the direction of the geostrophic flow in three of the cells shown is reversed!

In other sections the topics are not treated to the same depth and the book as a whole cannot therefore be considered as giving a balanced view of the subject. Notable weaknesses are an inadequate treatment of boundary effects and insufficient development of the description of oceanic water masses and T-S analysis. The chapter on tides is also disappointing. However, a comprehensive text to the standard of the best chapters would require a much larger book. As it stands it is overall a good text which goes a long way towards filling a persistent gap in the literature.

The Open University interdisciplinary course (S.334) in *Oceanography* is probably one of the best publications available at present, particularly in view of its impressive attempt to teach, rather than merely describe, the basic concepts of the subject. It comprises seven sections totalling 780 pages that deal with the physical, chemical, biological and geological aspects of the oceanic environment, as well as an appraisal of the complex political and economic problems which have arisen due to the exploitation of marine resources. The presentation of all the material follows a

format of discussion, questions, answers, comments, self-assessment and revision. It incorporates clear diagrams which have been either reproduced from well documented sources, or specifically constructed to illustrate the points under discussion. Each section concludes with a comprehensive list of references and suggestions for further optional reading.

To assimilate the contents of this course without too much difficulty a student would require a basic knowledge of at least two of the major sciences, and in fact would have a considerable advantage if one of these was in the field of geology since there is a distinct imbalance in favour of this subject. However, every effort is made to accommodate the less experienced by

punctuating the text with a liberal number of self-assessment exercises. Wherever possible the reader is encouraged to recall and compare different facets, which are in fact interrelated, of an oceanic phenomenon, although previously these might have been treated solely as a particular physical, chemical, or biological event. Indeed, the student should be prepared, for example, to consider such diverse oceanic processes as those that control: the broad eastern boundary currents with their associated regions of coastal upwelling; the balance between oxygen concentration and biological consumption; the rates of production and growth of commercial fish stocks; the sediment accumulation in the deep ocean;

and the present legal arguments regarding international straits, artificial installations and marine pollution. Whatever the topic, the information provided is invariably sufficient to enable the reader to gain an insight into the subject which is seldom achieved in the more superficial presentation of many oceanographic text books. The OU team have produced a most commendable script. □

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Isotope geology

Grenville Turner

Lectures in Isotope Geology. Edited by E. Jager and J.C. Hunziker. Pp.329. (Springer: Berlin, Heidelberg and New York, 1979.) DM49.00, US\$27.00

THIS book on isotope geology is the outcome of a two-week course of lectures to graduate and postgraduate earth scientists delivered by an international group of scientists at the University of Berne in 1977. It contains 24 chapters and covers topics related to the standard isotope dating methods (Rb-Sr, K-Ar, ^{40}Ar - ^{39}Ar , U-Th-Pb and fission tracks) as well as the principles and applications of stable isotope geochemistry. According to the preface and flyleaf it is intended to be an introduction to isotope geology aimed at geologists rather than isotope specialists. My own feeling is that it is not a book to read without some prior knowledge. As a textbook for a course on isotope geology it does not compare at all well with the excellent book by Faure, *Principles of Isotope Geology* (reviewed in *Nature* 272, 103 (1978)).

In fact, I was rather disappointed by this book. Before reading it I made a mental list of some of the topics in isotope geology which I regard as currently the most exciting. My list included the chronology and early evolution of the Earth's crust, the history of crust and upper mantle evolution based on modern studies of Nd-Sm, Rb-Sr and Pb isotopes, isotopic anomalies in the early Solar System and the chronology of the early Solar System. Apart from a short chapter on Archaean geochronology, an even shorter one on mantle geochemistry, and a discussion of crust and mantle interactions in the chapter on lead geochemistry, these exciting fields are virtually ignored. The contributions to the book are also rather patchy in the sense that 6 of the 24 chapters were of 5 pages or less (the shortest on the now defunct total lead

method was 2 pages!). Two authors were particularly guilty in this respect. I feel that the editors should either have rejected some of the contributions or demanded more substantial work. I realise that to construct a coherent whole from a list of 17 contributors is not an easy task. Nevertheless, it is an essential one for a book intended to be used as 'an introductory course'.

This review has emphasised the bad points of the book; like the well known egg it has some parts worthy of consumption

and several authors have given worthwhile summaries of particular fields. As a rough but not entirely correct guide, the usefulness of the chapters correlates with their length. Geologists and geochemists entering or already occupying the isotope field will therefore find parts of the book useful. However, considering its high cost I would encourage them to consult a library copy before buying. □

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Cloud physics

J. Latham

A Short Course in Cloud Physics. Second edition. By R.R. Rogers. Pp.248. (Pergamon: Oxford, 1979.) Hardback £14.50; flexi £7.25.

THIS short book is written for postgraduate students entering research in cloud physics. The structure of the book is conventional and logical. The initial chapters are concerned with meteorological thermodynamics. The appropriate thermodynamic laws and equations are first developed for dry air and are then extended to take account of the presence of water vapour. This leads to a discussion of static stability and air parcel buoyancy, which evolves naturally into an account of current understanding of mixing of air masses and theories of convection.

Three chapters are devoted to non-freezing clouds. The elements of homogeneous nucleation of water droplets are presented and then extended to take account of the role of condensation nuclei in the atmosphere. The subsequent growth of stable droplets by vapour diffusion is discussed and attention drawn to recent developments in the molecular kinetics of this phenomenon. The formation of

raindrops by the stochastic process of collision and coalescence of cloud droplets is considered. The parallel processes — heterogeneous nucleation, vapour growth and accretion — occurring in clouds containing the ice phase are then discussed. An account is presented of the relative growth rates of precipitation by the coalescence and ice crystal processes.

A chapter is devoted to various properties of precipitation particles. The size distribution of the hydrometeors occurring in natural rainfall and snowfall are discussed. The formation of satellite drops by the processes of aerodynamic breakup of raindrops or the collision of drop pairs is considered, and it is shown how the latter process produces spectra similar to those observed. The aggregation and breakup of snowflakes, and the precipitation rates encountered in various meteorological circumstances are then outlined.

A useful account is presented of the role of radar in meteorology and cloud physics research. A discussion of the basic principles of radar leads to development of the relevant equations linking the received power to the properties of the precipitation scattering the radiation. This chapter concludes with a description of types of radar display and special techniques employed in cloud physics, such as Doppler radar.

Two chapters entitled 'Precipitation

Processes' and 'Severe Storms and Hail' are devoted to more macroscopic aspects of cloud physics. Various precipitation systems are described, attention being given to the airflow which governs the release and distribution of rainfall. A brief discussion is presented of the efficiency with which cloud water is transformed into precipitation. A detailed account follows of the dynamics and life cycle of severe storms. This leads naturally to a description of the formation of hail and the energy balance equations which govern the growth of hail pellets.

The final two chapters contain skeletal

descriptions of current works in the important areas of weather modification and numerical modelling of cloud processes.

The problems for students presented at the end of each chapter are imaginatively devised and well balanced. It is helpful that in this second edition answers are given to odd-numbered questions. The book is modestly priced and serves as an excellent introduction to cloud physics. □

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Inorganic analysis

F.J.C. Rossotti

Vogel's Textbook of Macro and Semimicro Qualitative Inorganic Analysis. By G. Svehla. (Longman: Harlow, UK, 1979.) £14.95. *Practical Inorganic Chemistry.* By G. Pass and H. Sutcliffe. Pp.242. (Chapman and Hall: London, 1979.) Paperback £3.95.

FOUR editions of Vogel's textbook appeared between 1937 and 1954, the heyday of qualitative inorganic analysis in British schools and universities. Twenty-five years later, Svehla has produced a fifth edition, in an age when less time is devoted to practical chemistry in British curricula and the popularity of systematic qualitative analysis has waned. One of the benefits of a sound grounding in qualitative analysis is that students become familiar with a great deal of phenomenological inorganic chemistry, for example, colours, solubilities and reactions in solution. A backwards swing of the pendulum would now be timely.

The systematic qualitative analysis of some 44 cations and 47 anions is described. Length and contents of the new edition are much the same as before. Two short chapters on interfering anions and on paper chromatography in the previous edition have been assimilated into other chapters and there is some shuffling of order. However, updating seems to have been modest. Thus the section on solvent extraction remains weak and largely irrelevant in its detailed content. It might, for example, have been helpful to students to inform them that systems of qualitative analysis, which rely entirely on solvent extraction, now exist. In this connection, citation of key references (as in the Vogel *Quantitative Inorganic* text) would have been helpful in much of the book.

The most disappointing feature of the new edition is the still antiquated treatment

of reactions in solution. Thus ammonia and copper (II) ions do not yield a unique tetra-ammine (Dawson, 1900) but rather five mononuclear amines in stepwise equilibrium (Bjerrum, 1931). The blood-red colour produced on mixing iron (III) and thiocyanate ions has been variously attributed to $\text{Fe}(\text{NCS})_6^{3-}$ (third edition), $\text{Fe}(\text{NCS})_2^{+}$ (fourth edition) and now to $\text{Fe}(\text{NCS})_3$ (fifth edition). In fact, six thiocyanato complexes coexist in stepwise equilibrium and in relative amounts which depend upon the free thiocyanate ion concentration. Discharge of the red colour by fluoride ions is not due to the formation of a unique complex FeF_6^{3-} , but rather to an array of mononuclear fluoro complexes. Moreover, it is doubtful whether the hexafluoro species exists at all in aqueous solution. These typical outdated misconceptions about the nature of interactions between inorganic species in aqueous solution seriously mar an otherwise useful bench-book.

By contrast, Pass and Sutcliffe's text deals with the practical inorganic chemistry that has so largely replaced qualitative analysis in British university curricula. The current volume is a paperback reprint of the second edition of 1974. It contains a wide variety of preparative exercises, together with some reactions of transition metal ions and applications of some instrumental techniques. The interweaving of a certain amount of theory with the experimental instructions, together with the modest length and price of the book, must make it attractive for many courses.

Arbitrary choices of topic are inevitable if space is at a premium, but the omission of solvent extraction from a chapter on separation techniques, which contains ion-exchange, seems somewhat surprising. Again, it is regrettable that instruction on Job's method of continuous variations persists in the 2nd edition. This archaic method is of very limited applicability, again by virtue of stepwise complex formation. □

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Plasma physics

I.H. Hutchinson

Physics of High Temperature Plasmas. Second edition. By G. Schmidt. Pp.408. (Academic: New York, 1979.) \$29.50.

THE dilemma of most didactic texts, particularly in relatively rapidly developing subjects, lies between a presentation of the historical development of the discipline and an essentially axiomatic exposition along what are seen as the most logical lines. Few general plasma physics texts follow as completely the latter, non-historical approach as the second edition of *Physics of High Temperature Plasmas* by George Schmidt. This bias is emphasised by the deletion of the first edition's quite detailed bibliographies accompanying each chapter, in favour of a very brief list of books at the end. However, perhaps because of this approach, the new edition gives very little evidence of ageing.

The coverage is very wide, including treatments of particle motion guiding-centre approximations, the derivation of the CGL approximation, two chapters on magnetohydrodynamics, Vlasov wave and instability analyses, bounded plasma effects and touching on relaxation and collisions. The bulk of the material new to this edition is contained in a chapter on non-linear waves, providing a good introduction to topics not often covered by general texts.

The book is fully committed to being self-contained in its development. In this it succeeds rather well, hardly every specifically appealing to the reader's credence ('it can be shown'). However, there are definitely occasions when rigour is sacrificed in claiming the self-evidence of statements which, on reflection, are plausible though not obvious. Such points are inevitable and not necessarily detrimental. Indeed, greater attention to minutiae might have made the exposition too formal. As it is, while the many examples that are worked out in depth are mostly of direct experimental relevance, the uninitiated are left wondering just how the results really work out with a laboratory plasma. The feeling is enhanced by the fact that what few illustrations there are of the results in action are mostly of computational simulations.

A remarkable success of this book is that it covers such a broad range of topics with significant depth in just four hundred pages. This is achieved, on the one hand, by a very happy choice of examples and lines of development of the subject. On the other hand, though, the prose is compact, sometimes terse, and the mathematical

development inexorable; so that all but the most mathematically accomplished student must find it heavy going at times. Nevertheless, there are many valuable physical insights to be gained and we rarely lose sight of the physics behind the equations.

There are an annoying number of errors and misprints for a second edition.

"Stellerator" is a typographical error since it appears elsewhere correctly, but "Tokomak" seems deliberate and is neither a consistent transliteration of the Russian nor in conformity with general usage.

There is not really a wide choice of general graduate level plasma physics texts. Teachers will welcome this quite up to date

edition and researchers and students continue to appreciate its insights and breadth. □

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Basic organic chemistry

John Mann

Fundamentals of Organic Chemistry. By A.N. Nesmeyanov and N.A. Nesmeyanov. Pp.484. (MIR Publishers/Central Books: London, 1978.) £4.50 each, £16 for set of 4 volumes. *Organic Chemistry.* By D.J. Pasto and C.R. Johnson. Pp.542. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) Paperback £10.35. *Qualitative Organic Analysis.* By W. Kemp. Pp.183. (McGraw-Hill: New York and London, 1979.) Paperback £4.85. *An Introduction to Organic Chemistry.* By J. Carnduff. Pp.194. (Wiley: Chichester, UK, and New York, 1979.) £8.50.

THERE are no weighty tomes or glossy American textbooks under review this year. Instead, a Russian attempt in four, slim volumes, to cover the fundamentals of organic chemistry; a laboratory handbook of organic chemistry; a book of qualitative organic analysis; and an advanced school text.

The four-volume Russian work, *Fundamentals of Organic Chemistry*, by A.N. Nesmeyanov and N.A. Nesmeyanov is (I quote from the introduction) "designed for systematic study of Organic Chemistry, and covers a considerably wider field than a normal university treatment". Certainly the coverage is broader than in the average UK or American texts, and is more akin to that of Finar (*Organic Chemistry*, two volumes, Longmans: Harlow, UK, 1951) in its first edition. This resemblance extends to the old-fashioned representations of structures and stereochemistries, excusable in the ancient version of Finar, but not in a modern textbook.

Volume one commences with a full mathematical treatment of the theory of chemical reactions, and later does the same for electronic structure. Standard (in some cases antiquated) methods of preparation of saturated aliphatic compounds are then given, together with their main reactions, with not a curly arrow in sight. There are some good tables of physical constants, a

rare sight in modern textbooks of organic chemistry; and the volume concludes with a discussion of the classical chemistry of unsaturated aliphatic compounds.

This leads, in volume two, on to optical isomerism, and some very poor representations of chiral molecules. It is here that the comparison with modern western textbooks is so stark: one only has to think of the splendid illustrations in Cram and Cram (*Essence of Organic Chemistry*; for review see *Nature*, 278, 82; 1979), for example, to appreciate this fact. The reader is then led through sections on sugars (flat structures only), amino acids and polypeptides (no stereochemical structures at all), and alicyclic compounds. To be fair, this latter subject is dealt with in far greater detail than in any comparable text. The volume concludes with a chapter on physical methods of structure elucidation, comprising sections on mass spectrometry (here the reader is hurled straight into an exposition of Russian peptide sequencing using MS), nuclear magnetic resonance (again weak on fundamentals), and brief sections on infrared spectroscopy, and polarimetry. The comparisons with western textbooks are again rather unflattering.

Volume three includes aromatic and heterocyclic chemistry, and coverage of both topics is very extensive (295 and 121 pages, respectively). Some Russian specialities are stressed: many pages on the stereoisomerism of substituted biphenyls, and 44 pages on condensed aromatic systems.

In the final volume there is a comprehensive, if somewhat antiquated, treatment of organometallic chemistry, with a particularly extensive section on metal carbonyls (usually confined to inorganic texts). There is little mention of synthetic utility: hydroboration merits one page, whereas the Wittig reaction gets one mention in volume one, and half a page in this volume. Similarly, the section on carbanion chemistry contains no mention of current synthetic methodology. Terpenoids and alkaloids then receive a classical treatment, and the structures are particularly archaic here; but there is more steroid and alkaloid chemistry than in most student texts. However, the relevance of these secondary metabolites to pharmacology and ecological chemistry is ignored completely. The final chapters include discussions of nucleic acids, enzymes, and cofactors; and this is quite well done, apart

from an appalling photograph of the myoglobin molecule (one of the few photographs in the book).

At its best this work is comprehensive though rather antiquated; but the overall impression is one of dullness — it lacks the vital spark and visual appeal of most western textbooks.

D.J. Pasto and C.R. Johnson have, in their new book *Organic Chemistry*, produced an excellent laboratory handbook for undergraduate chemists. The book is in three parts: basic laboratory techniques, spectroscopic methods, and qualitative analysis. The introductory chapter in part one starts from first principles, and leads the novice experimentalist through sections on laboratory safety, elementary first-aid, general equipment and its uses, a solvent list, and yield calculation. This is followed by a chapter on techniques of separation and purification, from recrystallisation, sublimation, and distillation, through to a good section on chromatography which includes HPLC. Part one concludes with a chapter on physical characterisation which is concise but adequate. It is worth comparing this part of the book with the first part of Vogel (*Textbook of Practical Organic Chemistry*; also reviewed last year: 278, 82). This far weightier tome is much more comprehensive, but far less readable, whereas Pasto and Johnson have provided an introduction to the classical methods of organic chemistry in a form which students might even enjoy reading.

The second part commences with ultraviolet and visible spectra, then proceeds to a discussion of infrared spectroscopy, all of which is more than adequate for undergraduates involved in structure elucidation. The NMR section is very good, and includes ¹³C-NMR, NOE, and shift reagents, as well as all of the fundamentals; and the subsequent section on mass spectrometry is excellent. There are seventeen useful NMR problems (¹H and ¹³C), and ten mass spectra to interpret. Overall, the treatment is as good, if not better, than the standard texts of the day: Williams and Fleming (*Spectroscopic Methods in Organic Chemistry*; McGraw-Hill: New York and London, 1973), and Kemp (*Organic Spectroscopy*; Macmillan: London, 1975).

The final part deals with qualitative analysis, and once again the coverage is adequate, rather than extensive as in Vogel; but unlike the latter, IR and NMR

data are interspersed to show how modern spectroscopic methods and wet analysis can go hand-in-hand. The book concludes with a section on use of the research literature. Throughout the book there are good reading references, and it deserves to become a sort of bible for undergraduates taking courses in experimental organic chemistry; but it probably will not achieve this exalted position, as at £10.35 for a paperback, there are cheaper alternatives.

One of these is by W. Kemp (*Qualitative Organic Analysis*), who has successfully integrated wet analysis and modern spectroscopic techniques, but the coverage is not quite so comprehensive as that of Pasto and Johnson. The tables of derivatives are, however, marginally more extensive. The section on spectroscopic methods is much poorer, and includes only the bare essentials of each technique. The aim of the book is nonetheless realised, in that it shows qualitative analysis as a vehicle for learning functional group chemistry. On balance, a chemistry under-

graduate would probably do better to buy Pasto and Johnson, whereas ancillary students should find Kemp's book adequate for their needs.

The fourth book, *An Introduction to Organic Chemistry* by J. Carnduff, seeks to present organic chemistry for advanced level school students, from an electronic point of view. Thus the standard reactions of organic compounds are discussed with reference to the fate of the electrons involved. This is a refreshing departure from the norm, as most advanced level school texts seem afraid to include mechanisms and curly arrows. There are seven chapters which cover the fundamentals: 'electron accounting', nomenclature, stereochemistry (including chirality — perhaps a bit ambitious at this level), electronegativity, delocalisation, and classification of reaction types. This is accomplished very effectively, and is followed by chapters on organic compounds, including a useful chapter on organometallic species, as well as the usual

list from hydrocarbons to carbonyl compounds by way of alcohols and amines. The section on aromatic chemistry is particularly good. Problems appear at the end of each chapter, with answers at the end of the following one. The final chapter summarises what has been said about ionic reactions. This is a book full of good basic organic chemistry presented in a modern (mechanistic) fashion, and schools will probably buy a cheaper paperback version. My one reservation is the virtual absence of examples showing the industrial and biological relevance of organic chemistry. The Nuffield advanced level books go to the other extreme, with almost total exclusion of mechanism. Surely, a compromise can be reached — perhaps next year? □

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Fluid mechanics

T.N. Stevenson

Fluid Mechanics. By H.C. Lowe. Pp.228. (Macmillan: London, 1979.) Paperback £3.95.

FIRST-YEAR engineering courses in fluid mechanics are chosen from a vast range of topics. The material found in these courses would fill many volumes, and consequently any one volume of this size is unlikely to be adequate for any one course.

Each chapter in the book includes a short description of the physics and a cursory look at the theory for a particular topic. This is followed by a number of examples and specimen solutions. Some of the examples rely on the theory in this or earlier chapters, but most of them require a much deeper understanding of the subject. Questions are taken from the examinations of the North Staffordshire Polytechnic and the Council of Engineering Institutions. The author knows the syllabus for these courses and has made the approximations expected in those examinations. For the benefit of other students the author could have indicated how more accurate solutions could be obtained to some of the problems.

The book is written in note form with some of the symbols incomplete due to poor type. At least two of the examples have omissions which make them dimensionally incorrect and the vector notation used is not always correct. Some partial derivatives have been typed as total

derivatives. The sections on dimensional analysis, wakes, vortex shedding, and on turbulence are misleading. The explanation of Buckingham's π theorem is incomplete and the definition of laminar flow is wrong.

There are scores of books covering parts of first year undergraduate courses in fluid mechanics. Probably not one of these covers exactly the same topics as this text. There is an interesting set of examples in the

book. However, in view of the omissions and errors in the explanation of the physics involved, I cannot recommend the book to students. □

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Classical mechanics

J.W. Humberston

Intermediate Classical Mechanics. By J. Norwood, Jr. Pp.417. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) £14.30.

THE author's justification for writing another undergraduate text on classical mechanics is his belief that the subject should not only be concerned with particles and rigid bodies, but also with many body systems. He has therefore included chapters on elastic bodies, statistical mechanics and fluid mechanics in addition to the usual topics contained in books on classical mechanics. Some of the topics in these chapters are occasionally discussed in mechanics books at this level (for example, *Mechanics* by K.R. Symon), but others, such as plasma physics and hydromagnetic waves, are not. A chapter on relativity theory is also included which gives a rather superficial account of special relativity and

only a very brief introduction to general relativity. Several short problems are set throughout the book, but no solutions are given.

The general level of presentation is somewhat higher than is usual for a first year course in mechanics in a British University, although anyone who has taken such a course should have little difficulty understanding most parts of the book. It is clearly written and very well produced and seems to contain very few misprints or errors. One rather unfortunate example of the latter, however, occurs in the discussion of Kepler's laws of planetary motion. The author states, and claims to prove, that the second law, the constancy of the areal velocity, is only true for an attractive inverse square law of force; it is, of course, true for any central force, being a direct consequence of the conservation of angular momentum. □

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Statistics and experimental design in psychology

Donald Laming

The Numbers Game. By J.G. Snodgrass. Pp.467. (Oxford University Press: Oxford, 1979.) £5.95. *Experimenting in Psychology.* By R. Gottsdanker. Pp.352. (Prentice-Hall: Hemel Hempstead, UK, 1979.) £9.45.

IN teaching statistics and experimental design to psychology students there is always the problem of maintaining the students' interest. Here are two very different approaches to this problem.

The Numbers Game is a conventionally ordered introductory text. It begins with four chapters on descriptive statistics and then proceeds to an exposition of the standard normal-variate tests; non-parametric procedures are presented in the final three chapters. The writing of individual chapters reflects a great deal of thought and experience in teaching students who may have but little mathematical background. The presentation is conceptually oriented, with important mathematical arguments placed in supplements at the ends of chapters, and the concepts are illustrated with examples. In its concern for communicating with the student *The Numbers Game* is to be commended. But, because of the conventional ordering of the material, the student must work as far as chapter 10 before he is able to appreciate in its entirety even the simplest experiment. As Gottsdanker puts it in his preface to *Experimenting in Psychology*: "... to treat various 'topics', such as *measures of behavior, subjects, experimental designs, and treatment of data* in separate chapters. When that is done, there can be no comprehensive knowledge about any kind of experiment until the last chapter is covered."

Experimenting in Psychology employs a completely different approach. It is organised around a graded sequence of example experiments. These experiments are not used to illustrate previously stated principles (as in *The Numbers Game*); rather, they "carry" the exposition. Each experiment presents a practical problem which is worked through in the text, and the solution to this problem exemplifies the principle which the author wishes to present. In the early chapters the experiments are necessarily simple, mostly concerned with applied problems. Regrettably some of these are artificial, made-up examples, which are never as interesting as real ones. But in the later chapters dealing with the more complex problems of design, the experiments are all recently published examples drawn from a

wide range of psychological subject matter. The reader thereby obtains some appreciation of the complexity of experiment needed in contemporary research and of why its design is important; in addition, as a by-product, the book encourages a catholic interest in scientific psychology.

Of these two books, I am confident that the second will hold the students' interest the more readily. From the outset it demonstrates the importance of experimental design in psychological research and provides the student with a motive for studying its technicalities. Dr Gottsdanker is to be commended for developing this new approach. But, at the same time, he has bent over backwards trying not to alienate those with a distaste for mathematics. The main text is entirely devoid of algebra and only a very little statistical theory is included, set in a series of statistical supplements placed at the end

of each chapter. The author has, by intention, written a book on experimental design alone, virtually without statistics. But the criterion of good experimental design is that the data can readily be analysed with respect to the questions of interest; so that the possibilities for design are dominated by the analytical techniques. Dr Gottsdanker could have slipped in much more about data analysis than he has; it is a pity — it would have made the book more widely useful.

There remains the possibility that these two books, so very different in approach, might actually complement each other and be successfully used in tandem. They will provide an attractive combination for any psychologist who teaches chiefly the use of normal-variate procedures. □

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Establishing psychology

O. L. Zangwill

Introduction to Psychology. By E. Hilgard, R. A. Atkinson and R. C. Atkinson. Seventh edition. Pp. 653. (Harcourt Brace Jovanovich: New York and London, 1979.) Hardback £10.35; paperback £7.75. *Basic Writings in the History of Psychology.* By R. I. Watson. Pp. 420. (Oxford University Press: New York and Oxford, 1979.) £5.95. *Psychology Survey, No. 2.* Edited by K. Connolly. Pp. 288. (George Allen and Unwin: London and Boston, 1979.) Hardback £7.50; paperback £3.95. *Brain Behaviour and Evolution.* Edited by D. A. Oakley and H.C. Plotkin. Pp.237. (Methuen: London, 1979.) Hardback £9; paperback £4.95.

THESE four books, two British and two American, are all concerned in one way or another with the teaching of psychology at University level. It is, however, virtually impossible to compare them directly on account of the very real differences that exist between the British and American systems of higher education. While the American texts are designed to meet the needs of College students taking an introductory course in psychology who may or may not wish to proceed further with the subject, the British texts are intended for second- or third-year students taking psychology as a main subject in an Honours Degree course in a British university. Although the teaching of psychology in Britain makes extensive use of American texts and journals, it cannot

be said that either of the two American volumes under review is likely to prove obviously appropriate for use in this country. This is not, however, to say that they are both without educational value or do not merit sympathetic consideration.

The Hilgard, Atkinson and Atkinson text, originally published in 1953 and already fairly well known in Britain, now appears in its seventh edition. As in the earlier editions, the authors explain that they have tried to write an introductory text for students who in their experience are more likely to be interested in what they consider to be "relevant to their lives, futures and the problems confronting society" than in the preoccupations of professional psychologists. This fashionable demand for "relevance" they have attempted to meet "without sacrifice of scientific rigour or scholarship". In fact, the book consists very largely of the standard stuff of contemporary academic psychology enlivened by some reference to topics such as hypnosis, psychotherapy and the effects of psychotropic drugs, which students are presumably expected to deem "relevant". In spite of this somewhat patronising attitude to supposed student interests, it must be said that the authors have produced an attractive text that presents the subject matter of experimental psychology intelligently and well. It may be surmised that it owes much to Dr Hilgard's admirable good sense and solid judgement and to his fortunate choice of collaborators.

Dr Watson's compilation of *Basic Writings in the History of Psychology* at all events makes no compromise with "relevance", as it might be supposed that few American students of introductory psychology would dissent from the celebrated judgement of Henry Ford. The book consists of some fifty extracts from

the writings of assorted philosophers and scientists, including Descartes, Locke and Helmholtz, who may be said to have laid the groundwork for the evolution of psychology as a science. It also contains extracts from the work of some thirty leading psychologists of the nineteenth and early twentieth centuries, mainly German and American although a few British. In his selection, Dr Watson seems to have been much influenced by E. G. Boring's views and follows closely the judgements expressed in his well known *History of Experimental Psychology*. As a result neither French nor Russian psychologists (with the exception of Pavlov, who would have hated to be called a psychologist) find inclusion.

While one may agree with Dr Watson that historical knowledge is of educational value, one may doubt whether the method he has chosen to represent it is a satisfactory one. Indeed it would seem to be modelled more upon *The Readers' Digest* than upon any serious contribution to historical scholarship. Nonetheless, there is just a hope that it might inspire an exceptional student to delve into some of the original sources. It is also exceptionally cheap by today's standards.

Let us now turn to the two British productions. *Psychology Survey, No. 2*, the second volume in a new series, follows closely the pattern established by Professor Brian Foss, who edited the first. It consists of fifteen chapters, each dealing with a single issue or area of inquiry in contemporary psychology. The (very varied) topics have been chosen by Professor Connolly on the grounds of their

timeliness and promise on the one hand and the fact that their authors are personally engaged in research in the relevant area on the other. These chapters have no explicit connecting link and may be thought to illustrate well the late Professor Gilbert Ryle's view that psychology is less a science than a consortium of inquiries and techniques that neither has, nor needs, a logically trim statement of programme. Nonetheless, the editor clearly hopes that his patchwork quilt will provide both stimulation and variety. In this, he is unlikely to be disappointed.

The individual contributions to this book vary very considerably in their range of coverage. Some deal with large areas of the subject as, for example, human engineering or psychopharmacology; others with special issues or topics, such as the theory of colour vision or motor activity mutants of *Drosophila*. In (almost) all cases, however, the authors clearly know what they are talking about and express themselves lucidly and well. In particular, there is a merciful absence of jargon. Like its predecessor, this book may be expected to receive a warm welcome from teachers of psychology and their students.

Lastly we have *Brain, Behaviour and Evolution*, a collection of longish essays expressly compiled to provide students of psychology or the social sciences lacking a background in the natural sciences with some understanding of evolutionary biology. The chapters are of two types, the first four providing basic information about the anatomy of the nervous system, the evolution and genetics of behaviour,

brain-behaviour relationships and neurochemistry in relation to evolution. The next five chapters are concerned with more specialised issues, including the evolution and functions of sleep, the relationship of brain size to intelligence (this is a particularly thoughtful and scholarly survey) and the ostensible functional asymmetry of the two cerebral hemispheres in man. To this last chapter Dr Roger Sperry appends a brief afterword on consciousness.

This book is on the whole well done and will undoubtedly be of help to the not inconsiderable number of students to whom it is directed. From an educational point of view, however, it must be insisted that such a book is no substitute for a basic grounding in the established biological sciences and one may well doubt the wisdom of allowing candidates to proceed to degrees in psychology or behavioural science without some previous grounding in the biological or pre-clinical sciences. If this should become an accepted convention, university departments of psychology would of course attract far fewer people than at present and staff and resources would correspondingly diminish. Nonetheless, the quality of the product might well be higher and the prospects for the subject brighter. Psychology would then have the chance to establish itself firmly in the consortium of biological sciences. □

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For the newcomer to nuclear physics

Daphne F. Jackson

Theoretical Nuclear Physics. By J. M. Blatt and V. F. Weisskopf. Pp. 864. (Springer: New York, Berlin and Heidelberg, 1979.) DM64; \$35.20.

THIS book was first published as a postgraduate textbook in 1952, twenty years after the experimental discovery of the neutron. Before its publication, newcomers to the study of nuclear physics would probably have used review articles published in the 1930s in *Reviews of Modern Physics* and *Handbuch der Physik* as their introduction to the subject, together with the more descriptive book by Bethe and Morrison.

Blatt and Weisskopf set out to give a complete presentation of the theoretical

concepts and considerations which must form part of any theory of nuclear properties and of theoretical techniques which should be used in the analysis and correlation of experimental data. The latter aspect was of particular importance because nuclear physics at that time was in much the same position as atomic physics some thirty to forty years earlier, with a substantial accumulation of spectroscopic information and low energy scattering data but no means of deriving the behaviour of nuclear forces or the properties of nuclei from more fundamental sources.

The authors began at the beginning by discussing the constituents of nuclei, the stability of nuclei, and the significance of the behaviour of the binding energy per nucleon as a function of mass number. They made the assumption that non-relativistic quantum mechanics could be applied to nuclei and proceeded to discuss the excitation of nuclear states and the implications of quantum statistics for nuclear systems. These are all topics which have now reached well down into the undergraduate syllabus for physics

students.

The major sections of the book which deal with two-body scattering at low energies and the basic character of the nuclear force and with the general theory of low energy nuclear scattering and reactions, were of great importance when first published and remain very valuable. It is remarkable that much of the notation and many of the illustrations have been carried on into later books by other authors. This confirms the success that Blatt and Weisskopf had in achieving their aim of making the subject understandable to readers equipped with a reasonable background in quantum mechanics. The section of the book dealing with the interaction of nuclei with electromagnetic radiation and the appendix on multipole radiation are outstanding.

The chapter on β -decay remains useful while that on α -decay is rather meagre. Fission is not covered in any detail because much of the relevant information was still classified at the time of writing. From the point of view of the modern reader, the least satisfactory sections of the book are

those concerned with the interpretation of nuclear spectroscopic data in terms of nuclear models. When the book was started the shell model had only just emerged and it was nearly ten years later that Weisskopf exposed the important role of the exclusion principle in limiting two-body collisions of the bound nucleons and so making possible the long mean-free-paths required for the existence of independent particle motion. It then became possible to understand how the repeated influence of the residual interactions not included in the averaged potential of the shell model could lead to the formation of the compound nucleus. The addition of a short appendix covering this point would have helped new readers to avoid unnecessary confusion.

The book inevitably contains little

discussion of reactions above 20 MeV and it is rather amusing to see energies between 10 and 50 MeV classified as "very high energies" and those above 50 MeV classified as "ultra high energies".

It is open to question whether the re-issue of a book which was written nearly thirty years ago, without any revision or even up-to-date commentary in footnotes and appendices, provides a real service to nuclear physicists. The book still provides a very good introduction to the theoretical techniques of low energy nuclear physics and could usefully serve as a background reader for a first major course on nuclear theory. The book would be of little further use to postgraduates working on nuclear structure theory or direct reactions but should remain of some value to experimentalists working on very low energy

reactions and electromagnetic interactions. Indeed, the book might now serve as a foundation for studies in applied nuclear physics.

From a less utilitarian standpoint, there are strong reasons for congratulating the new publishers for keeping this major work in print. It is a classic example of how to write a textbook in a newly developing field. The style is lucid and the authors were capable of being both imaginatively descriptive and searchingly critical. The mathematical formalism has an elegant, uncluttered appearance. This book is attractive to an extent unsurpassed by later works of comparable scientific complexity. □

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Atomic, nuclear and elementary particle physics

P.G. Murphy

The Structure of Matter: An Introduction to Atomic, Nuclear and Particle Physics. By R.M. Turnbull. Pp.266. (Blackie: Glasgow and London, 1979.) Paperback £7.95.

THIS book contains a concise account of atomic, nuclear and elementary particle physics, for the early years of an undergraduate course in science. It is written at a fairly elementary level compared with most of the numerous texts of this kind. It gives more space than is usual to elementary particles, justified by the inclusion of very recent developments of fundamental significance. Most of the book contains traditional material treated in an orthodox manner. It should therefore reach a very high standard to justify its addition to our libraries, or the expenditure of a large sum for a slim volume. Let us therefore look at the treatment of one of the most important parts of the subject. On page 96 we are told that "Schrödinger postulated a wave equation . . .", followed in the next sentence by equation 8.5, which is a wave equation; nothing is said to prevent the innocent student from believing that it is the Schrödinger equation. Unfortunately it is not (except possibly the relativistic form for a massless particle). The true Schrödinger equation does appear, two pages later, as a result of some unexplained manipulations on a harmonic wave. Then we are told that it is "known as the time-dependent form since . . . V is in general a function of both position and time". This is wrong; the

phrase refers to the wave function, not to the potential (which could well be zero). The next sentence says "Wave-particle duality is incorporated . . . since it . . . contains a potential energy term describing the interaction of a particle with its environment". This duality is inherent in the interpretation of the wave function and has nothing to do with the potential.

Tutors who have to eliminate these ideas will wish that this book had not been published. I have described only the worst faults I have found. In other parts we find

an inadequate treatment of the uncertainty principle, a long section on Wilson-Sommerfeld orbits which is an unnecessary difficult subject, again with misleading and inadequate explanations (it leaves us thinking that Sommerfeld's relativistic term explains fine structure correctly), and other inaccuracies. This book cannot be recommended. □

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Developments in physics

Leonardo Castillejo

The Structure of Matter. By S. Gasiorowicz. Pp.525. (Addison-Wesley: London, 1979.) £16.50.

IN 1933 the publication of Max Born's classical book *Atomic Physics* set a standard for a comprehensive yet simple introduction to the new ideas and developments in physics. Since that time the subject has grown so large that most authors choose to restrict themselves to one field such as relativity or quantum mechanics, solid state or statistical physics, and to provide within the chosen topic more mathematical details and worked examples to enable the student, not only to grasp the new ideas, but also to calculate things for himself.

In this textbook on *The Structure of Matter* Dr Gasiorowicz has combined both these aims. He includes all the topics listed above, together with a wide range of simple

applications and illustrations in related fields. The mathematical requirements are few; basic calculus and the use of matrices. The physical arguments are presented very clearly and followed up with explicit calculations, often on a simple model, so that all the details can be worked out. The crucial features which generalise to the real problem are then clearly emphasised.

The book is divided into six parts. The first covers relativity. This is an excellent and lucid exposition of the essential ideas and provides a working knowledge of Lorentz transformations, relativistic kinematics and even some transformations of electromagnetic fields. The second section on statistical physics is based on a mixture of statistical distribution and kinematic theory, derives the Boltzmann distribution, with some applications, and discusses black-body radiation. I was unhappy that the concept of temperature, which is so fundamental, was introduced rather superficially in terms of the ideal gas law.

There follow three sections on quantum mechanics; the first explaining the early models, then a self-contained and beautifully clear section formulating quantum mechanics up to the harmonic oscillator and finally a more advanced section including angular momentum, the

hydrogen atom and spin. In the final part of the book the methods of quantum theory, statistical physics and relativity are used to describe and explain a broad spectrum of physical phenomena. The examples are well chosen to give an overview of modern physics as well as to provide opportunities to extend calculational techniques. For example, the discussion of electromagnetic transitions and selection rules also provides a derivation of

time dependent perturbation theory, and the calculations of specific heats of phonons and electrons provide an introduction to Bose and Fermi-Dirac statistics. This last part introduces the reader to atomic and molecular physics, solid state, nuclear physics and elementary particles. The latter topic is treated in more detail than the others and ends with a discussion of quarks, colour and charm.

This book is exciting to read, yet

designed for instruction and as a course text. There are many good examples at the end of each chapter. It is one of the best introductory textbooks to modern physics which I have seen and it deserves to be widely used. □

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Analytical chemistry

T.S. West

Analytical Chemistry. By D.J. Pietrzyk and C.W. Frank. Second edition. Pp.700. (Academic: New York and London, 1979.) £16.50.

A DETAILED examination of the text of this book shows that in many respects it is rather like the legendary 'curate's egg'. At first sight there are many excellent features of planning and intention such as material on sampling, choice of analytical method, literature on analytical chemistry, units, standards, preliminary operations, and so on; but, unfortunately, these are vitiated by lack of penetration into the subject or by a loose approach. So, what looks promising when one first looks at the list of contents, turns out to be little more than a run-of-the-mill treatment. In the sense that

there are references to the edicts or regulations of bodies such as the FDA, EPA, APHA, ASTM, and so on, which is, of course, perfectly appropriate for the student mass market in the USA, the book is nevertheless a US national rather than an international publication.

It is considerably less welcome, however, to find the use of the 'Formality concept' predominating in the book and, even though lip service is paid to SI, it has to be said that 0.1F H_3PO_4 is more inconsistent and confusing than continued use of 'ml', 'litre', and so on, which are, at least, still in common use throughout the world. It is also noticeable that principal references are made almost exclusively to American papers and books and, indeed, that there are very few references to the original literature throughout the text. Students who use this text are consequently likely to receive little training or introduction to a concept which the authors apparently value highly. According to page 18: "The literature of analytical chemistry, as in any other scientific area, is the life blood. The books provide the newcomer with the

required background while the journals provide a vehicle for critical discussion about the old and the new." Yet on the very next page one of the leading international journals is incorrectly given.

The subject matter is treated fairly fundamentally and goes into the conventional techniques of gravimetry, titrimetry (given as "volumetry"), fairly well. The treatment of optical procedures such as flame spectrometry (still showing detailed diagrams of a total consumption burner), atomic absorption and fluorescence spectroscopy is so rudimentary that it is almost without value: similarly polarography. The separation section on ion exchange and chromatography is more satisfactory; but the solvent extraction chapter, which includes a solitary incomplete reference, is also lacking in penetration.

This is not a book that I would recommend with any degree of confidence.

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Solid-state chemistry

J.N. Murrell

Structure and Bonding in Solid State Chemistry. By M.F.C. Ladd. Pp.326. (Wiley: New York and Chichester, UK, 1979.) £16.50.

THIS is a welcome book on solid-state chemistry, for I am sure that the subject gets short treatment in most chemistry courses. The difficulty faced by an author in this field is to decide what to include and what to omit. The subject cannot be taught without reference to gas phase molecular structure and to chemical bonding theory but these are topics adequately covered in other monographs. If this background material is omitted then I suppose that there is the danger that the book will either be rather thin or will have to include detail which is too specialised for an undergraduate text.

Dr Ladd has chosen to include a substantial amount of background material on basic quantum mechanics and the theory of the covalent bond (over 70 pages in all). He also includes 10 pages of appendices covering the thermodynamics of electrolyte solutions, required, as far as I can see, only for brief discussion of the solubility of ionic compounds. My own inclination would have been to direct the reader to other books for these topics because I think it diverts attention from the main direction of the text.

Chapter 1 is titled "Preamble" and gives an introduction to the structure of solids. In contrast to my view expressed above I found this section surprisingly thin on the experimental and theoretical aspects of diffraction. For example, I found no reference to neutron diffraction and its relevance to the position of hydrogen atoms in solids. The book would certainly not be adequate to cover the material necessary for undergraduate chemistry teaching of diffraction.

Chapter 2 covers ionic crystals comprehensively, reflecting one of Dr Ladd's research interests. There is a short section

on colour centres. Chapter 3 deals with covalent compounds but only one page out of seventy deals with covalent solids directly (diamond, for example), the rest being used for the background material already referred to.

Chapter 4 is titled "Van der Waals' Compounds" and contains a brief description of intermolecular forces and their relevance to inert gas solids, organic molecular solids and donor-acceptor complexes. Chapter 5 covers metallic compounds and contains an elementary treatment of band theory; the free-electron model, Brillouin zones and Bloch theory. Each chapter presents a set of problems and solutions are given at the end of the book.

In summary, I feel that the balance of the book is not ideal but it should still be very useful reading for students of chemistry and chemical physics. □

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Astronomy textbooks

David W. Hughes

The Solar System. By J.A. Wood. Pp.196. (Prentice-Hall International: Hemel Hempstead, UK, 1979.) £5.05. *Galaxies: Structure and Evolution.* By R.J. Tayler. Pp.203. (Taylor and Francis Wykeham Publications: London and Basingstoke, 1979.) Paperback £4.50. *The Astrolabe.* By H.N. Saunders. Pp.12. (Science Studio: Oxford, 1979.) £4.75. *Projects and Demonstrations in Astronomy.* By D. Tattersfield. Pp.331. (Stanley Thornes: Cheltenham, UK, 1979.) *Astronomy: Activities and Experiments.* By L.J. Kelsey, D.B. Hoff and J.S. Neff. Pp.187. (Kendall/Hunt: Dubuque, Iowa, 1979.) *Activities in Astronomy.* By D.B. Hoff, L.J. Kelsey and J.S. Neff. Pp.142. (Kendall/Hunt: Dubuque, Iowa, 1979.) *Astronomy: From the Earth to the Universe.* By J.M. Pasachoff. Pp.200. (W.B. Saunders: Philadelphia, London, Toronto, 1979.) (Plus *Teachers Guide*.) *Exploring the Cosmos.* By L. Berman and J.C. Evans. Second edition. Pp.89. (Little, Brown: Boston and Toronto, 1979.) (Plus *Instructor's Manual*.) *The Macmillan Dictionary of Astronomy.* By V. Illingworth. Pp.378. (Macmillan: London and Basingstoke, 1979.) £8.95.

THIS year's crop of astronomy textbooks can be easily sorted into three groups which, for want of better, can be labelled advanced, experimental and simple.

Two books fall into the advanced section; both are on specific astronomical topics and both are aimed at the second- and third-year university undergraduate. Both are excellent in their own way and both are extremely good value for money. The first is *The Solar System* by John A. Wood, an ideal introduction for all astronomy, geophysics and physics students. Wood had an extremely difficult job in front of him — express in about 50,000 words and 125 figures what you think is of major importance in the Solar System. Now one easy way out is to isolate the planets from the Sun and the neighbouring stars in the Galaxy. Wood didn't do this, thank goodness, and this makes the book even more praiseworthy. He also decided to discuss, chapter by chapter, the unifying features of planets. So we don't get a chapter on each and an insulation of our knowledge of a single planet from the overall picture. Wood considers broad topics, the motions of planets and their interrelations, the surfaces and their evolution, planetary interiors and atmospheres, rocks from space (meteorites and lunar samples), the Sun, solar evolution and the origin of the elements and finally the origin of the Solar System. This book is going to be a firm

Particle physics

Norman Dombey

Elementary Particle Physics. By D.C. Cheng and G.K. O'Neill. Pp. 423. (Addison-Wesley: Reading, Massachusetts, 1980.) \$29.50.

THIS is a very nice brief introductory text to the subject with roughly half devoted to electromagnetic and weak interactions and half to strong interactions. It is up to date: not only does charm enter together with strangeness in Chapter I but even the SLAC experiment of summer 1978 showing parity violation in electron scattering is quoted.

Nevertheless, the book is solid rather

favourite in universities for years to come. Maybe in the next edition Wood could help the lecturer out when it comes to tutorial and exam time by including a set of questions. Also the suggestions for further reading are a bit dated.

The second advanced book is *Galaxies: Structure and Evolution* by R.J. Tayler, a new title in the excellent *Wykeham Science Series*. Despite their intended aim — to bridge the gap between school and university studies — this book is again at mainstream second- and third-year university level. It is an excellent companion to Tayler's other two books in the series, *The Stars: Their Structure and Evolution* and *The Origin of the Chemical Elements*.

Galaxies are getting more and more popular in astronomy possibly because the number of known galaxies is increasing considerably as telescope instrumentation becomes more sophisticated. I never cease to be amazed at the statistic that there are about as many galaxies in the Universe as there are stars in our own Galaxy. Tayler doesn't cut corners in his book. Galactic properties are discussed with physical and mathematical precision. Considerable emphasis is given to the one galaxy that has been observed well, the one we are in, and there are chapters on observational results, stellar dynamics and the interstellar medium. Careful consideration is also given to the problems of estimating galactic mass and size and assessing the effects of chemical evolution. Other chapters deal with the different classes of galaxies and the origin and evolution of galaxies and the Universe.

This book will make galactic astronomy more accessible to many students and Professor Tayler is to be well congratulated for this.

Finally in the advanced section we have *The Astrolabe* by H.N. Saunders, a plastic folder which contains a 12-page booklet and an assembled, 14.5-cm diameter, white

than fashionable and in spirit belongs to the late 1960s and early 1970s (this is not meant as a criticism) rather than the present. C,P and T-invariance; SU(3), (4) and (6); form-factors and structure functions; quarks and partons; dispersion relations and Regge Poles are all treated in some depth. Gauge theories are mentioned but not explained; so is the unification of weak and electromagnetic interactions; but QCD perhaps wisely is absent.

I will certainly recommend the book to my students, both undergraduate and graduate. There are, however, several errors in the text of the edition I received which need correcting. □

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and clear plastic astrolabe. The astrolabe was invented in Alexandria around 400 AD and was used by astronomers for over 1,200 years. It gives the times of rising and setting of the Sun and certain specific stars throughout the year and their positions in the sky (that is, altitude and azimuth) at any time of the day and night. The astrolabe in the Saunders package has been designed for use at latitude 50° North but will still give useful answers within two degrees or so of this. If you want to know how astrolabes work and wish to become acquainted with such terms as retes, rules, plates, tympan, almucantars, heliacal risings and alidades this is just for you. There are 32 stars on the plate and the booklet is clearly written and contains many worked examples of astrolabe uses. The Saunders instrument is well made, durable and will stand up to a considerable amount of student handling. It would provide the basis of a very reasonable laboratory experiment for the more historically minded. A brief comparison can be made with another astrolabe package. In 1974 Roderick S. Webster produced an 8¾" diameter, six section astrolabe kit, printed on gold cardboard and die cut so that the sections press out and don't have to be cut out (in 1974 it was \$18 and obtainable from Paul MacAlister and Associates, Box 157, Lake Bluff, Illinois 60044). Six plates were included, for latitudes 30, 36, 42, 49, 52 and 56° North. It was decorated to conform with Renaissance practice. Webster's astrolabe looks more like 'museum' examples but is much more fragile than the smaller plastic Saunders one. Webster's booklet did stress the historical aspect more and had an excellent bibliography.

Let us now turn to the experimental aspects of astronomy. Like many other sciences, astronomy is both practical and theoretical and the majority of students studying the subject spend a considerable



A shining arc of the Sun's chromosphere (taken from *The Illustrated Encyclopaedia of Astronomy and Space*; Macmillan: London)

time doing observational and laboratory assignments. At my university the first-year students have to do 15 over a period of two terms. When it comes to preparing the instruction sheets for these projects I dip deeply into a whole range of books and manuals and when new books on astronomical experiments come onto the market I must admit that I buy them indiscriminately. Each book invariably contains a few good ideas usually distilled from the painful experience of the writer who has a similar job of organising laboratory and observing work for a large class of students. The British student doesn't usually expect to have to buy a laboratory manual. This is often not the case in America.

Projects and Demonstrations in Astronomy by D. Tattersfield is written for the overcast astronomer, and the author offers a range of projects that can be done indoors using only the most modest equipment and a modicum of mathematical skill. Many of these projects would be suitable for advanced level (about seventeen years old) students. In reading the book I came across many good ideas but too few projects which I would adopt in their entirety. I thought that too much use had been made of line drawings of photographic plates and spectra. This gives the student too little impression of the problems of measuring spectral lines on real plates. Often in astronomical spectroscopy the apparent width of the line varies as one moves along it. Also when it comes to measuring the distances between star images on plates the images are not points but diffuse and sometimes irregular disks. Reproductions of the original photographs can be produced fairly easily, as has been shown in the excellent series of laboratory exercises published by Sky Publishing Corporation from their journal *Sky and Telescope*. Tattersfield does this for the North American Nebula and I think should have done it more often.

More emphasis should also have been given to the errors in the quantities obtained from the graphical and numerical calculations. A student acquainted with the mathematics required to do these exercises

should also know about standard deviation and the problems of fitting linear functions to small sets of data. In this context I am very worried when students are encouraged to plot the logarithm of the mass against the absolute magnitude for Sirius A and the Sun and then told "Draw a straight line through the two points on the graph. This is the mass-luminosity relationship." The author in the extensive "Solutions" section at the end of the book then adds data points for Capella A and Kruger 60A and inserts a much more reasonable line. I think I will use Tattersfield's book quite a bit, but only as a jumping off point, and with caution.

Astronomy: Activities and Experiments by Linda J. Kelsey, Darrel B. Hoff and John S. Neff is a revised and updated edition of the original 1971 manual which was published by the University of Iowa. After reading this book, two points become very clear. Firstly that the authors have had years of experience in the job of making laboratory exercises interesting and exciting for first-year university students and in dealing with the general range of student problems. Secondly they are first rate experimental scientists who know well the joys and frustrations of experimentation and the disciplines that must be developed when it comes to analysing and presenting the results. They end the brief section of suggestions for writing laboratory reports with the curt statement "Think before you write". Throughout the book it is obvious that the authors did just that. The book contains forty exercises, fairly evenly split between telescopes and observational techniques, coordinate systems and time, Earth, Moon and planets and the Sun, stars and galaxies. It is clearly presented, and well illustrated with a host of photographic reproductions. Each experimental text is subdivided into sections labelled purpose, references, introduction, procedure and discussion questions. It is an excellent book and I recommend it very strongly. It has been specifically designed for a two semester astronomy course at American universities but will be of inestimable use to all university, college and upper school teachers.

The book has spawned a baby brother. *Activities in Astronomy* by D.B. Hoff, L.J. Kelsey and J.S. Neff is aimed at the one-semester introductory astronomy student and is a shortened and somewhat simplified version of the previous book, containing only 25 exercises. The standard of presentation is just as good.

Now to the 'simple' books, by which I mean the ones designed for the non-mathematical American arts students market. I have been looking at three this year and these are Jay M. Pasachoff's *Astronomy: From the Earth to the Universe*, *Exploring the Cosmos* by L. Berman and J.C. Evans, and *New Horizons in Astronomy* by J.C. Brandt and S.P. Maran. *Horizons* and *Cosmos* are both second editions and Pasachoff's book is a slightly more historical version of his *Astronomy Now* which was a shorter version of his *Contemporary Astronomy* which was a shorter and no algebra and trigonometry version of his *University Astronomy* . . .

Where do we go from here? All the books cover the same areas of astronomy and are profusely illustrated with photographs of planets, stars, galaxies, clusters, and so on. If I were a student I would leave the choice of book to my course tutor. He has probably designed his teaching and his approach to astronomy around a specific text. The tests and examinations that must be passed will be based on that specific text. The scholar buys the book, learns the work, passes the exam, gets older and forgets astronomy. But look at it from a different angle. How should astronomy be taught to non-mathematical students? These three books illustrate two basic approaches. One is to treat astronomy as a simple story, which can begin historically, or at the edges of the Universe or at the Earth's surface or with our nearest star the Sun, and to tell the story with the aid of pictures. Pasachoff does this and so do Brandt and Maran. Both books do it well and colourfully, but I found myself time and again asking the question "Is it science?". The second approach is to treat astronomy not as a story, but as a science, a great science, the first science. The author can vary the difficulty of his approach but he never forgets that he is dealing with a science subject, a subject of experiment and hypothesis, of fruitful paths and blind alleys, a subject in which the mysteries of the unknown increase as our knowledge grows. Berman and Evans treat astronomy as a science. If I was teaching American arts majors about astronomy and trying to tell them what it is really all about I would use a book like Berman and Evans' *Exploring the Cosmos*. I would buy this book for some of the line drawings alone. It contains very little mathematics. That which is there can be understood by the most arty of art students given a bit of motivation. J. Robert Oppenheimer said "I believe most strongly in the nobility of this great effort

to understand nature". Berman and Evans stress the how of astronomy as opposed to the other authors who spend too long simply describing the what.

Valerie Illingworth has edited *The Macmillan Dictionary of Astronomy* from contributions commissioned from a host of British professional astronomers. Dictionaries can be easily judged by asking two questions. The first is "Is it in?"

Ignorance forces you to open the dictionary and the dictionary is only useful if it has an entry on the subject you are looking up. Secondly, "Does this entry tell you what you want to know?". The answer to the first question was "yes". The Macmillan dictionary nearly always had it in. Butler matrix, Bw stars, ylem, YY Orioris stars were all there. I only caught it out by straying into planetary geological

features (grabens, horsts, and so on) and I should not have been looking these up in an astronomy dictionary anyway. I answered the second question in the affirmative too. So the conclusion is simple, if you want a good astronomy dictionary get this one. □

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Aerospace environment

T.B. Jones

The Upper Atmosphere and Solar-Terrestrial Relations. By J.K. Hargreaves. Pp.298. (Van Nostrand, Reinhold: Wokingham, UK, 1979.) £7.25.

THE launch of the first satellites in the late 1950s stimulated the study of space physics which has expanded rapidly since that time. The Earth's outer environment, or 'near space', is a particularly important and interesting region from both scientific and engineering viewpoints. It is the region where strong interactions with solar radiations and particles occur and where ionised particles can greatly influence man's activities.

Dr Hargreaves' book provides an excellent introduction to the aerospace environment. It is intended primarily for

undergraduate use and in this respect it fills an important need, as there are relatively few books available on the subject at this level. The present volume provides a broad picture of the Earth's environment, beginning at the base of the ionosphere and extending outwards to the magnetospheric boundary. The structure and behaviour of the ionosphere and magnetosphere are discussed in detail and these topics form the major part of the book. The interaction of the Sun's emissions with the Earth's environment is of fundamental importance in understanding the behaviour of both the ionosphere and the magnetosphere and full coverage of this subject is included. In particular, a detailed account is given of solar disturbance phenomena and their spectacular consequences in the aerospace environment. Mathematical formulation has been kept to a minimum and is only introduced where essential to the understanding of a particular section. Chapters have been included on experimental techniques and on the engineering significance of the various regions described.

The material is well illustrated throughout and many cross-references have been included. In several cases numerical estimates of the magnitude of various parameters (for example, electric currents and fields) are included which help the reader relate them to his everyday laboratory experience. Copious references to more advanced literature are included at the end of each chapter.

The author has succeeded in presenting an integrated account of the wide range of phenomena which occur in the Earth's outer environment. He has done this in a clear and concise style which makes the book particularly attractive for undergraduate use. The work will also appeal to the more specialised reader who will find it helpful to have the wide range of topics, together with many references to source material, contained in one compact volume. □

T.B. Jones is Reader in Physics at the University of Leicester, UK.

Solar energy

D.O. Hall

The Sun. By D.K. McDaniels. Pp.271. (Wiley: New York and Chichester, UK, 1979.) Paperback £6.50.

THIS is a good book and certainly can be recommended as an introductory text for a course on solar energy, but . . . Why is it that so many books, articles, and so forth, on solar energy ignore the most important use of solar energy today, that is, the energy from biomass which daily provides the equivalent of 20 million barrels of oil (equal to USA oil consumption) — probably because such solar energy use mostly occurs in developing countries where it is of crucial importance. But it is not recognised that currently, for example, the USA obtains about 2% and Sweden about 10% of their total energy

from biomass. Enough said!

The first three chapters discuss the overall energy problem, although it is heavily biased to the US situation. There are excellent chapters on the Sun and Universe and on solar radiation, and there are also discussions on economics.

The second half of the book describes solar energy applications for heating, cooling and electric power generation. The presentation of principles of operation, and the examples given, are very well thought out and clearly written with good diagrams and figures. The index and references are useful; the problems at the end of each chapter will also be helpful in teaching.

In short, a book to be recommended, as much experience in repeated teaching of a solar energy course to beginners is evident in the presentation. "The emphasis is entirely upon developing a qualitative approach of the subject" — this has been achieved. □

D.O. Hall is Professor of Biology of King's College, London, and Chairman of the UK Section of the International Solar Energy Society.

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Speech physics

C. J. Darwin

The Physics of Speech. By D. B. Fry. Pp.148. (Cambridge University Press: Cambridge and New York, 1979.) Hardback £9.50; paperback £3.50.

THE study of speech brings together an extraordinary variety of people. There are not just the phoneticians, old and new, transcribing and measuring, training their ears and improving their syntheses, but also a growing number of satellites: computer scientists and electrical engineers intent on recognising and synthesising speech automatically, psychologists trying to understand how on earth we all manage to produce and perceive speech at all, speech pathologists helping those who can't and the theoretical linguists, phonologists and

beyond, wondering what it all means.

Students in all these fields need to know the fundamentals of speech, but their teaching presents real problems as the engineer's meat is the pathologist's poison. Professor Fry's book is not for engineers. He manages, successfully, to explain the principles of the physics of speech assuming no mathematical ability in his reader (the only equation used is the definition of the decibel, and Fourier is not even mentioned). Nevertheless, all the necessary ideas are presented in a clear if not very sprightly way. Any student who has read the book carefully will understand the notion of a spectrum, appreciate the distinction between a sound source and its subsequent filtering, know what formants are and how to interpret a spectrogram, and will have some rudimentary knowledge of the acoustic cues to the more important phonetic distinctions. There are, of course, minor flaws, but nothing is seriously misleading.

The competition with which Fry's book has to contend is Ladefoged's *Elements of Acoustic Phonetics*, first published in 1962 and still available in paperback from University of Chicago Press for around two dollars. Ladefoged deals with wave analysis at greater length than Fry, illustrating his chapter with many clear diagrams of waves and spectra. Fry, with some justification, neglects the waveform for the spectrum. I suspect that students will find Ladefoged's treatment of this topic more lively than Fry's, and will appreciate his use of fewer words and more diagrams. But Ladefoged spends appreciably less time on actual speech sounds and their underlying production mechanisms, so that, faced with a real spectrogram, his reader would be considerably more baffled than Fry's. □

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Variegated manifestations

D. Rosen

Aspects of Biophysics. By W. Hughes. Pp.362. (Wiley: New York and Chichester, UK, 1979.) £11.95. *Biophysical Science.* By E. Ackerman, L.B.M. Ellis and L.E. Williams. Second edition. Pp.634. (Prentice-Hall: Englewood Cliffs, New Jersey, and Hemel Hempstead, UK, 1979.) £18.20.

HUGHES quotes a US National Academy of Sciences study which argues that "the classical subdisciplines of biology [that is, zoology, botany, and so on] are insufficiently instructive as approaches to current understanding and appreciation of life in its variegated [sic] manifestations". He uses this as a valid justification for cutting through the range of biological phenomena in an orderly way, with the order determined by those physical phenomena which can be discerned among the biological ones. Ackerman and his co-authors find the subject organised in almost the same sequence as that found by Hughes, but they tackle it in the reverse order. The two books are at just about the same level, textbooks suitable for senior undergraduates or junior graduate students.

The problem of teaching biophysics now is akin to the problem of teaching biochemistry about 50 years ago. Then, the question was whether any students would have the requisite background in chemistry and biology: they were likely to have one but not both. Now, the question is whether they have the background of physics, chemistry and biology: they may well have the first two or the last two, but not all

three. The two books considered here both affect, in the enthusiasm of their prefaces, to be appropriate to all classes of readers. In a rough way, however, it may be said that Hughes' book is more suited to the student with the physics-chemistry background and Ackerman's to the student with the biology-chemistry background.

Hughes starts with atoms and molecules and with X-ray diffraction and electron microscopy as the techniques of studying the most elementary parts of living things. He builds upwards. He goes on to describe the physics of proteins and nucleic acids, and then membranes and mitochondria, so leading to physical aspects of cellular function and organic function, and finally to still larger problems of living matter. What I particularly liked in his approach is the way he pushes a numerate, mathematical description into quite elementary accounts of the various topics he deals with, from enzyme action to vision. When the topic itself has a well established mathematical formulation, he takes full advantage of it. In his account of nerve action potentials, for example, he gives brief but adequate derivations of cable theory and the Goldman equation for transmembrane potential before going on to obtain the Hodgkin-Huxley equation. However, this is strictly the physics or physical chemistry of the matter — it comes with only the barest introduction and practically no account of the biological consequences. What I found most distressing in Hughes' book were the misprints and spelling errors, starting on line 3 of page ix, as quoted above, and continuing liberally through the text, striking alike at formula and English word.

Ackerman, Ellis and Williams, in the second edition of a book originally by Ackerman alone, have kept to the plan of

the first edition. This combines a partly historical approach with some pedagogical insight into what might tempt a student to give attention to topics in biophysics. The Preface proposes Helmholtz as the originator of biophysics and the first chapters deal with Helmholtz' major interests, hearing and vision. The development is then, as it were, analytic in contrast to Hughes' synthetic approach — the electrically sensitive tissues of the body are considered, leading on to other interaction of cells with physical stimuli, to the physical features of cellular function, to the constituent parts of cells, to biological macromolecules, and to the thermodynamics of biological function. In further contrast to Hughes, Ackerman and his colleagues seem to pull in mathematical explanation with some reluctance when it can hardly be avoided, but prefer a descriptive approach. In their account of nerve action, they give a brief explanation of the Hodgkin-Huxley equation but do not mention cable theory or even the Nernst or Goldman formulae for transmembrane potential. In most other cases, however, they end up by giving much the same physics in much the same mathematical form as is given by Hughes, but accompany it with fuller verbal explanation and better indications of the implications for the study of biology. Ackerman and his co-authors devote the final part of their book, a sixth of the whole text, to biophysical techniques and instrumentation and to medical applications of biophysics. That this section, seventeen years later, is the only one which required major recasting from the first edition, shows how well Ackerman judged his original text; and the second edition preserves the confidence and balance of the first.

From the comments made here it can

perhaps be inferred that these two books, although coming to biophysics in opposite ways, are not complementary: they are just different and each has its virtues. Ackerman is nearly twice as long (and nearly twice as expensive) as Hughes, and so contains lengthier accounts, but nearly all topics found in one also appear in the other. However, though I can imagine few

students with a biological background preferring Hughes to Ackerman, there are some students from physics who would prefer Ackerman's approach to that of Hughes. My own preference is marginally in favour of Hughes — I found his style the livelier of the two, his approach to topics more engaged, and the references he provides more interesting and research-

oriented. Both books are to be recommended, however, as serious introductions to biophysics, and both are better than the two or three comparable texts which have recently appeared. □

D. Rosen is Head of the Department of Biophysics and Bioengineering at Chelsea College, University of London, UK.

Introductory immunology

George Feinberg

Immunology at a Glance. By J.H.L. Playfair. Pp.35. (Blackwell: Oxford, 1979.) £2.25. *Immunology Simplified.* By T.R. Bowry. (Oxford University Press: Oxford, 1979.) £2.50. *Textbook of Immunology.* By B. Benacerraf and E.R. Unanue. Pp.298. (Williams and Wilkins Company: Baltimore, 1979.) \$10.95.

THE only thing these three books have in common is the word "immunology" in their titles. No three authors could have taken three more diversified approaches to their common subject. Yet, this is not to fault any of them, since immunology has become so complex an author must take a calculated decision on how he can best present it to the would-be learner.

J.H.L. Playfair's *Immunology at a Glance* chooses to do it essentially with diagrams (sketches, the author calls them): a set of 34, in fact, which starts with the "Scope of Immunology" and then proceeds stepwise in complement cascade fashion, each diagram 'activating' the next till the "terminal assembly" of three diagrams representing "Altered Immunity". The sequence is logical and each diagram is accompanied by a brief — I would say too brief — explanatory section, as well as a useful listing of definitions.

But the title is misleading. *Immunology at a glance* the book certainly is not. The diagrams are often complex: one picture may be worth a thousand words, but not when it tries to express a 'thousand' ideas. Even with the accompanying explanations, most of the diagrams require a study session rather than a glance. That said, it is a good book, based on a novel approach, but ill-served by its title, which suggests it is a casual book for the beginner. In fact, in his preface the author states "this is not a book for immunologists". I dispute this! I see its greatest potential as an *aide memoire* to the professional immunologist and, especially, to the teacher of immunology, who, more than anyone else, must try to grasp the whole picture. I suggest a more appropriate title for this book would be: "An Atlas of Immunology".

Alas, as in all first editions, some errors have crept in: such as a definition of lysosome which gives the impression the

macrophage is its sole source; and the diagram on "Anaphylaxis and Allergy", which has bradykinin emerging as a mediator from the mast cell. I must also note my sorrow at one glaring omission: the failure to give due consideration to the structure and characteristics of antigens, without which there would be no immunology.

The book by T.R. Bowry is antipodean to that of Playfair. *Immunology Simplified* it certainly is; some may feel it is oversimplified. It reduces diagrams to a bare essential and relies, instead, on a narrative-style text to make the immunological feast palatable to the uninitiated. In this it largely succeeds, but — perhaps inevitably — at the sacrifice of any profundity. Without too much effort, it could be transformed into a book of popular immunology for the layman.

But perhaps therein lies its strength: it follows a logically flowing pattern, setting forth the fundamentals in three brief chapters, before ranging over the consequences — good and bad — of the activation of the adaptive immune system. Adding to the sense of simplicity — "extreme simplicity" is the publisher's assessment on the back cover — is the small-page format and the large, open print. This is a book which succeeds in living up to its title; and if it is 'simple' immunology the reader is seeking, he need go no further in his quest.

The last of the trio, Benacerraf and Unanue's *Textbook of Immunology*, comes closest to the traditional idea of a college textbook. With its informal offset lithography it gives the impression of being the original lecture notes of an immunology teacher. Perhaps this is not surprising, as it "was originally organised from the teaching materials . . . (used) as part of the introductory course in immunology of the Harvard Medical School curriculum". The best praise I can give it is that it certainly lives up to the standards one would expect from an institution of Harvard's repute.

Again, we have a type which is large and easy on the eye. This makes the mastering of the wealth of up-to-date information in the book a less formidable prospect. The development of the subject is classical and, to my way of thinking, logical in devoting a whole chapter to a consideration of antigen, before launching into the immune response it induces. Perhaps less logical is the presentation of the complement system

long after a series of chapters in which a familiarity with its workings would be useful; but in a book that so elegantly sets out the precepts of immunology, this is mere quibbling. Particularly lucid presentations of complex subjects are the chapters on transplantation biology, immune regulation and immunogenetics. Diagrams are sparse, but clear and pertinent. I found no obvious errors of omission; nor, at a quick reading, any of commission. Pleasing, too, is the short list of both classical and current references appended to each chapter.

So here we have three books collectively catering for a wide variety of tastes and needs. It is for the reader to choose that most suited to his immunological appetite and/or dietary requirements. □

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Participating in perception

F. W. Campbell

Sensation and Perception. By S. Coen, C. Porac and L. M. Ward. Pp.514. (Academic: New York, San Francisco and London, 1979) Hardback \$14.95; £9.75; paperback £6.50.

THIS textbook has several unusual features which make it a particularly useful teaching tool. Firstly, it is extraordinarily well illustrated with numerous clearcut diagrams to distill succinctly the relevant information. To illustrate the properties of colour vision there are also a number of colour plates. One of its strongest features is the Demonstration Boxes, which contain instructions for the reader to undertake numerous simple experiments. For example, pouring out a glass of water reflected in a ladies' hand-mirror. To quote from another Box, "use two white plastic spoons (like those probably available in any campus cafeteria) to produce a Ganzfeld by placing the bowls of the two spoons over each eye as shown in the accompanying figure". Again, sit in your motor car, turn on the radio and start the engine. Change the engine speed and note

the effects of the engine noise on the quality and perception of some classical music. This encouragement of the reader to participate does much to deepen their understanding of the text.

To cover the whole range of sensation and perception has required three authors. Yet the style is very uniform and well integrated. Indeed, another unusual feature is to intermingle the different sensations rather than segregating each one to its individual section.

For the newcomer there is a comprehensive glossary of specialised terms, words and units. There are 23 pages of references containing some 500 scientific papers to enable the reader to study in depth any particular point. There is also a good author and subject index.

Recent advances are often handled by inserting a Special Topic, such as, How to Calculate d-prime, or, What is the Neural Response? or, The Modulation Transfer Function. This enables the newcomer to skip these special points on his first reading.

The publishers are to be congratulated on producing such an attractive volume for a remarkably low price. □

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How the mind works

Sandy Lovie

Cognitive Psychology. By W.A. Wickelgren. Pp.436. (Prentice-Hall: Englewood Cliffs, New Jersey and Hemel Hempstead, UK, 1979.) £11.

THIS is the latest offering from the ever flowing pen of one of the leading lights in human information processing and cognition. In a (relatively) brief compass Wickelgren deftly sketches in most of the live areas and issues of this loosely articulated and most exciting area of psychology. From such traditional areas as perception (both visual and auditory), imagery and attention, thinking, reading and long- and short-term memory, to the more novel topics of semantic memory, Wickelgren has assembled a most persuasive body of evidence to support his modest contention that "Cognitive psychology is concerned with the general principles of how the mind works". Moreover Wickelgren's ability to synthesise material and to disambiguate the closely argued efforts of most of today's brightest workers gives the reader

the exciting and restless feeling of being at the edge of current knowledge (few references are earlier than 1960, most are from the middle to late 1970s).

Of course, Wickelgren cannot hope to avoid the larger questions hanging over the subject: for example, is it structure *and* process or structure *or* process; is it all happening in here or out there; what about the issues of application and ecological validity; how far can we push the computer analogy? Perhaps it is inappropriate to ask so committed a member of the cognition club to bother too much about these issues, as their lengthy (and usually ponderous) consideration tends to spoil the fun in describing the experimental infighting. But these problems are neither trivial nor vacuous simply because of their low rating on the excitement scale.

Three final points: the chapter objectives and summaries are useful both for insightful and memorial purposes; thank God for the lack of references to Thomas Kuhn, paradigms, normal science, and so on; please when can we have a paperback version for our impoverished students? □

Sandy Lovie is Lecturer in Psychology at the University of Liverpool, UK (Acting Head 1979-80).

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Behaviour of experimental animals

B.J. Sahakian

Animal Behaviour in the Laboratory. By P. Silverman. Pp.409. (Chapman and Hall: Andover, UK, 1979.) £15; paperback £8.50.

THE author has attempted to write a simple, informative, and interesting account of the methods available for the observation and quantification of the behaviour of experimental animals. The dust-jacket indicates that the text is suitable for use by "second and third year undergraduates studying animal behaviour and psychology; to postgraduates and to industrial research workers in pharmacology and toxicology laboratories". Its 25 chapters cover a range of tests currently used by researchers interested in determining the effects of drugs on behaviour. The tests include those for the investigation of both conditioned and unconditioned behaviours, and the emphasis is on the behaviour of rodents. The chapters are varied and discuss such topics as ethics, experimental design, physiological psychology, drug screening, central nervous system pharmacology, motor activity, exploratory behaviour, self-

administration of drugs and brain stimulation, classical and operant conditioning, and social behaviour.

Although there are some excellent texts for the expert or the advanced student in this area, this book could possibly fill a need for the beginning student or the worker in industrial pharmacological or toxicological research wanting to acquire behavioural skills. Unfortunately, however, though the author has chosen his topics well, their treatment is disappointing. The style of writing is sometimes vague and often lapses into homespun philosophy, where opinions are not substantiated by reference to published research. This tendency is irritating when such important issues as the widespread abuse of barbiturates as sleeping-pills in the UK is discussed for example, page 37. In general the text could be supplemented by more references, particularly in certain chapters (e.g. chapter 11) to work done after 1970.

Balancing these faults, the summaries at the ends of most chapters are clear and concise, and the different indices (General Chemicals, Species, and Author) are a useful feature. Finally, it is obvious that the author has a sincere concern for ethical standards in procedures used with experimental animals, a matter of considerable relevance for a general audience. □

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